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Behavior of Red Snapper, Lutjanus Campechanus, in Relation to Trawl Modifications to Reduce Shrimp Trawler Bycatch.

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BEHAVIOR OF RED SNAPPER, *LUTJANUS CAMPECHANUS,* IN RELATION TO TRAWL MODIFICATIONS TO REDUCE SHRIMP TRAWLER BYCATCH

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
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in

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by
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Most importantly, I would like to express sincere appreciation to my parents, Claude and Gene Reeve, and the rest of my family, for encouraging me to pursue my goals. Heartfelt thanks to my husband, Barton, for all his inspiration and assistance during this endeavor.

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ABSTRACT

Behavioral responses of young-of-the-year red snapper, *Lutjanus campechanus,* to alterations in water flow were examined in the laboratory and the field in an effort to facilitate their release from shrimp trawls.

Experiments with red snapper, collected by divers, were conducted in a racetrack flume. Four vertical and two horizontal mesh and solid panel types were examined. Four snapper (out of 96) escaped with vertical panels and thirteen fish (out of 48) exited with horizontal panels. Escapes occurred primarily with solid panels containing 0.95-cm holes drilled at 5-cm intervals. However, snapper that escaped with solid horizontal panels frequently went back into the net.

The reduced water flow areas created by the panels appeared to trigger a territorial response in the juvenile snapper. Frequently, individuals that were behind the panel would attack other snapper, thus limiting access to the escape openings. Based on these experiments, panels do not appear to be an effective mechanism to induce young-of-the-year red snapper to exit trawls.

Other experiments examined the behavior of red snapper in response to increasing and constant fish density, the presence of a trawl-webbing reef, and water flow. Agonistic activity increased as fish density increased, peaked at a density of 11 snapper per 0.16 m^3 of water, then declined. The presence of a reef under no-flow conditions increased agonistic encounters when one or two snapper defended the territory. Agonistic behavior increased with water flow over no flow conditions because fish defended reduced-flow areas.

The snapper appeared to form dominance hierarchies in the absence of a reef, and when excluded from the reef by the resident snapper. Disruptions by the resident snapper may have prevented the dominance hierarchy among nonresident

snapper from stabilizing, since the number of agonistic acts remained high. In contrast, agonistic activity among a constant number of snapper declined over time. These snapper appeared to establish a dominance hierarchy quickly and required little subsequent agonism to maintain the hierarchy. Agonistic behavior may reduce the ability of young-of-the-year red snapper to escape from bycatch reduction devices that create areas of reduced water flow near escape openings.

CHAPTER 1

INTRODUCTION

The red snapper, *Lutjanus campechanus*, is a reef fish primarily distributed from North Carolina to Key West, Florida, and along the Gulf of Mexico shelf to the Campeche banks of Mexico (Rivas 1966). Red snapper populations have declined over recent years, and assessments of Gulf stocks indicated this species was being seriously overfished (Goodyear and Phares 1990; Goodyear 1995).

There are substantial commercial and recreational fisheries for red snapper in the Gulf of Mexico. Declining commercial catches from 1983 to 1990 led to the institution of quotas in recent years, as well as size and creel limits on recreational harvests (Goodyear 1992). The 1997 yearly total allowable catch (TAC) of red snapper in the Gulf of Mexico was set at 4140 t, distributed between the recreational (49%) and commercial (51%) fisheries (Gulf of Mexico Fishery Management Council 1998). The Gulf of Mexico Fishery Management Council voted to retain this TAC for 1998 because of concerns that a TAC reduction would cause severe social and economic impacts to the commercial and recreational fisheries.

In addition to the commercial and recreational harvest of adult red snapper, large numbers of juveniles (50-160 mm TL) are caught by the commercial shrimping fleet (Bradley and Bryan 1975; Gutherz and Pellegrin 1988). Bradley and Bryan (1975) suggested that increased towing speeds and more efficient trawls are capturing more juvenile snappers than in previous years. The annual catch by commercial shrimpers in the U.S. Gulf of Mexico from 1972 to 1981 was estimated to be 4.5 to 5.1 million juvenile red snapper(Gutherz and Pellegrin 1988). Estimates for 1972 to 1985 were 10.9 million snapper (Nichols et al. 1987). Shrimping effort declined 5.8% in 1993 and 10% in 1994 when compared against the 1984 to 1990

mean (Gulf of Mexico Fishery Management Council 1996). Bradley and Bryan (1975) advised that further research on life history strategies and populations of red snapper was essential since the numbers of trawl-caught juveniles may be small compared to the total population.

Some additional management options available for improving populations of red snapper include seasonal and area closures, large fish exclusion by TED's (Turtle Excluder Devices), and methods to reduce juvenile bycatch in shrimp trawls (Gulf of Mexico Fishery Management Council 1996). Juvenile snapper are found in trawl samples nearly year-round (Gutherz and Pellegrin 1988), and Hendrickson and Griffin (1993) concluded that seasonal closures would be ineffective in reducing red snapper shrimp trawler bycatch. Natural and artificial reef areas and underwater obstructions created by offshore oil and gas production facilities may also provide protection from trawling for juvenile snapper. However, Link (1997) estimated that the total amount of untrawlable bottom in National Marine Fisheries Service (NMFS) statistical zones 10-21 of the Gulf of Mexico (excluding the Florida region) in less than 64 m depths was approximately 185,000 ha, or roughly only 1.7% of the total trawlable area. Although red snapper reduction occurs with TED's, and TED's are currently required on most shrimp trawls in the Gulf of Mexico, the effects of current TED regulations on red snapper bycatch were considered negligible (Gulf of Mexico Fishery Management Council 1996). Declining stocks of red snapper and other fishery species have fostered development and testing of modifications to shrimp trawls to reduce bycatch, termed bycatch reduction devices (BRD's). These BRD's are designed to take advantage of behavioral differences between fishes and shrimp. In contrast to most fishes, penaeid shrimp are not able to maintain orientation against the current in the forward part of the trawl. The movement of the trawl generally

"propels" some shrimp from the center of the trawl into the codend and impinges other shrimp against the trawl webbing where they usually tumble down the webbing panels and into the codend (Watson et al. 1992). Fishes are generally more able to maintain position in the trawl, and some fishes can swim forward and escape through openings in the net.

Bycatch species from shrimp trawls in the Gulf of Mexico are often similar in size to the shrimp, and shrimp may compose as little as 10% of the total catch (Seidel 1975). Because of the similar size and abundant bycatch, many of the BRD designs that were used successfully in other shrimp fisheries, where fishes were typically larger than the shrimp and much less abundant, have proven ineffective. For example, a horizontal separator panel yielded a 75% reduction in bycatch, but lost 30% of the shrimp (Seidel 1975). Seidel (1975) tested six modifications of the Pacific Northwest shrimp separator trawl, which has a vertical separator panel and several chutes for fish escapement. Shrimp losses ranged from 9.1 to 63.5%, and fish reduction ranged from 37 to 83.5%; however, the modification with the best fish reduction had a shrimp loss of 63.5%. The lowest attainable shrimp loss (6%) from a trawl with vertical separator panels of varying mesh had a 45% bycatch reduction (Watson and McVea 1977).

Two of the most effective BRD designs in Gulf of Mexico waters are the fisheye and the extended funnel (Watson et al. 1993; Rogers et al. 1997a). The fisheye is a half-cone with an oval end often constructed of aluminum roundstock. The forward edge of the cone is typically inserted into the top of the net with the circular frame opening facing the codend and protruding inside the trawl. The inside portion of the cone is covered with webbing, the outside is open to allow fishes to escape through the oval opening (Watson et al. 1993, Rogers et al. 1997a). The

extended funnel design incorporates a polyethylene mesh accelerator funnel that is extended on one side, and surrounded by a section of large square meshes for fish escapement (Watson et al. 1993, Rogers et al. 1997b).

Modifications to original BRD designs may improve reduction rates. For example, fishermen in Texas have recently developed a BRD modification (the Jones/Davis BRD) which significantly improved fish reduction from the extended funnel design and could potentially improve fish reduction rates of other BRD's. This modification incorporates a webbing cone behind the funnel which acts as a fish stimulator, discouraging fishes from passing into the aft portion of the bag and improved fish reduction (Watson et al. 1997).

BRD's have been suggested as the most apparent solution to the red snapper bycatch problem (Bradley and Bryan 1975; Goodyear et al. 1990) and recent legislation requires the use of the top-opening fisheye BRD in shrimp trawls in federal waters of the Gulf of Mexico beginning in mid-May 1998. The 1998 red snapper TAC recommendation was tied to this legislation, and fishing could be halted if shrimp trawler bycatch was deemed excessive. Only 66% of the TAC would be available from January 1 through August 31, 1998. The remainder would be released for harvest only if this was accompanied by at least a 60% reduction in red snapper bycatch mortality. Reduction amounts between 50 and 60% would result in release of 10% of the remaining TAC for each additional percent above 50% (Gulf of Mexico Fishery Management Council 1998).

Depending on the species present in the trawl, BRD's often have quite variable reduction rates. For example, the extended funnel and fisheye designs effectively eliminate hardhead catfish, *Arius felis,* with reductions of 80 to 90% in offshore (Watson et al. 1993) and 42 to 50% in inshore waters (Rogers et al. 1997a,b).

However, because of behavior, it is difficult to induce juvenile red snapper to leave trawls. It is thought that this is due to their strong attraction to reef-type structures. Although reduction rates for larger (> 130 mm TL) juvenile red snapper can be as high as 40 to 80% for these two BRD designs, little reduction occurs for juveniles smaller than 120 mm (Branstetter 1997).

Burst and sustained swimming speeds generally increase with fish size (Blaxter and Dickson 1958). Small (60 to 100 mm) snapper have a sustained swimming speed of 0.2-0.3 m/s and are capable of burst speeds of 0.6-1.0 m/s (Branstetter 1997). Smaller snapper may be unable to sustain swimming against the water flow inside the trawl and be forced into the codend (Watson et al. 1992).

Many of the BRD's are designed to create reduced-flow areas within the trawl. The flow of water in the trawl may be an important factor in developing modifications to improve gear selectivity (Watson 1988). In theory, fishes entering these areas of reduced flow should be physically able to escape through nearby openings. However, juvenile red snapper presented with escape openings frequently do not exit trawls unless there is some type of stimulus such as quick movements of the net, reduction in trawling speed, or fish crowding that are associated with haulback (when the nets are hauled back to the vessel). Snapper that do exit during a trawl will often swim back into the escape opening, or draft behind trawl webbing on the outside of the net or even behind the codend. Although snapper appear to be attracted to reduced-flow areas, this does not seem to induce them to exit trawls.

This research was designed to examine the behavioral responses of smaller juveniles, not only to modifications in water flow, but also to other stimuli that commonly occur in shrimp trawls. Understanding the importance of disturbances and varying fish densities could prove important in developing BRD designs that reduce

the bycatch of fishes of management concern. It is also essential to determine what factors affect agonistic behavior in juvenile snapper. Intraspecific interactions between juveniles may affect the mortality rates of individuals exposed to shrimp trawl fisheries.

CHAPTER 2

BEHAVIORAL RESPONSES OF JUVENILE RED SNAPPER, *LUTJANUS CAMPECHANUS,* TO VERTICAL AND HORIZONTAL PANELS

Introduction

One of the BRD designs previously tested by the Harvesting Systems Branch of the National Marine Fisheries Service (NMFS) was a side-opening separator design which used vertical panels (aluminum frames covered with mesh) to slow the water flow and attract fishes to escape openings (Watson et al. 1993). This design had only limited success, and it was hypothesized that the angle at which the panel was set affected the water-flow characteristics behind the panel and subsequently influenced escapement.

Laboratory experiments were designed to test two panel angles to examine the influence of panel angles and materials on juvenile red snapper escapement rates. Because the material of which the panel was constructed could potentially influence water flows and thus fish escapement, four different vertical panel types with side-escape openings were examined. These consisted of three different webbing configurations and a solid panel with holes drilled at intervals to allow water to pass through the panel. These various configurations allowed different amounts of water to pass through the panel. Juvenile red snapper in shrimp trawls were frequently observed to remain near the bottom of the trawl (NMFS videotapes). These observations suggested that snapper might exit more readily from a bottom escape opening, therefore two types (mesh and solid) of horizontal panels were also examined. If an effective panel material, configuration, and angle could be discerned from these laboratory studies, this information could perhaps be incorporated into a new BRD design for field testing.

Methods

Collection and Maintenance of Snapper

Juvenile red snapper were collected off the coast of Pascagoula, Mississippi, in depths of 14 to 21 m. Divers collected most snapper with a hand trawl with a 1.83-m headrope length, 7.9-mm stretch mesh in the body, and 4.8-mm codend mesh. Snapper were collected over trawl-webbing reefs during the first year of the study. These reefs were constructed of 3 m^2 sections of trawl webbing. The webbing was anchored at each corner to the bottom. Additional snapper were collected by trawling from the NMFS vessel *Caretta* during the first year of the project. A few snapper were caught by divers with a slurp gun and a clear vinyl collecting net. During the final year of the study, the small trawl was held open by two divers swimming along the edge of rubble reefs while a third diver herded juvenile snapper into the trawl. Snapper were transported to the Louisiana Universities Marine Consortium (LUMCON) facility in Cocodrie, Louisiana, in ice chests equipped with 12-V aerators and cooled by small sealed bags of ice.

About 300 snapper that ranged in length from 45 to 75 mm (TL) were kept at LUMCON over a two and a half year period for use in the experiments. New fish were collected each year so individuals were only used in a limited number of experiments. Snapper were held in two to three 0.74-m high, 1.68-m diameter circular fiberglass tanks. Tank water was run continuously through a biofilter, ultraviolet sterilizer, and heater-chiller circulator. The snapper were fed several times daily with TetraBits® bite size food bits (TetraWerke, Germany), gel food, or pelleted hybrid striped bass food (Burris Feeds).

Flume Tank

Behavioral experiments were conducted in a Plexiglas racetrack flume (Figure 2.1). The working channel was 8.5 m long and 81.3 cm wide. The flume sides and bottom were constructed of 1.9-cm-thick seamless Plexiglas. Water flow in the flume was driven by a tracker design drive with 29 lexan paddles mounted on rotating sprockets supported by an aluminum frame. This design provides a smooth uniform flow in the working channel. Water depths in the flume were maintained at 32 cm. At this depth, the flume contained approximately 5240 L of water. Flume water was continuously circulated through an ultraviolet sterilizer located on the drive channel. To minimize stress to the snapper, salinities and temperatures of holding tanks and the flume tank were maintained as similarly as possible (generally 32‰ and 22 °C). Both ends of the flume working channel were blocked off by 2.54-cm square plastic mesh to retain fish in the experimental chamber.

The sides and bottom of the flume were covered with black felt to minimize reflections and distractions. A felt-covered wooden frame was attached to the outside of the working channel to allow the snapper to be videotaped without disturbing them. Three 100-watt incandescent bulbs were suspended above the tank and separated from the tank by a two-layer filter of gray fiberglass screen mesh to evenly distribute the light. Light output was regulated by a rheostat and was maintained at the minimum lux necessary for operation of the video camera. All experiments were taped by a Sony CCD-TR600 High 8-mm video camera recorder (Sony Corporation, Japan).

Panels

Horizontal and vertical panel configurations were tested in a rigid frame constructed of 0.64-mm rods (Figure 2.2) and surrounded by 3.5-cm stretch nylon

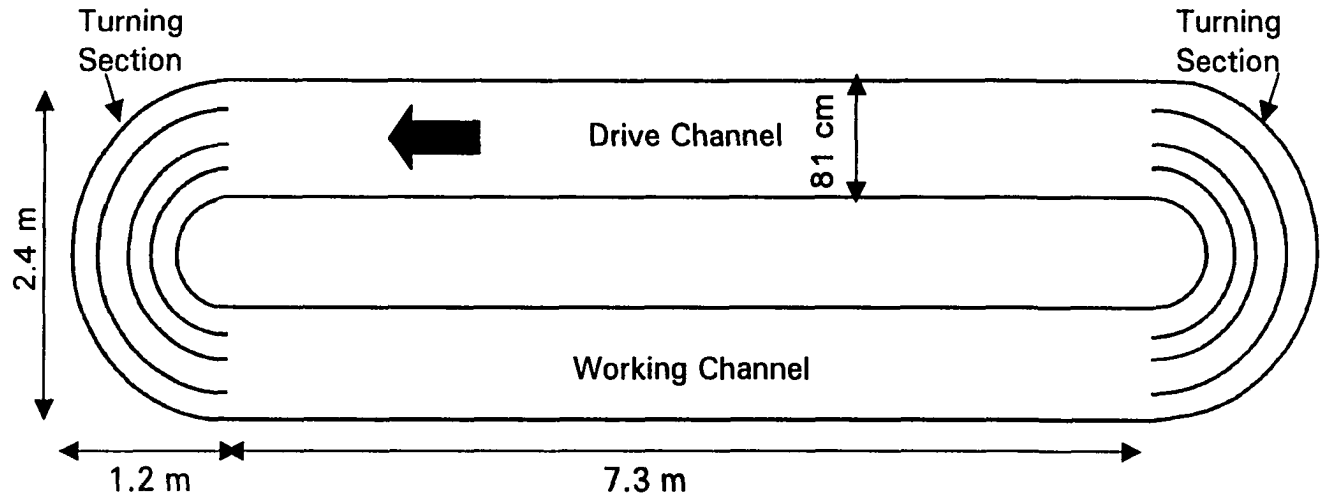


Figure 2.1. Diagram of racetrack flume. Large arrow is direction of water flow.

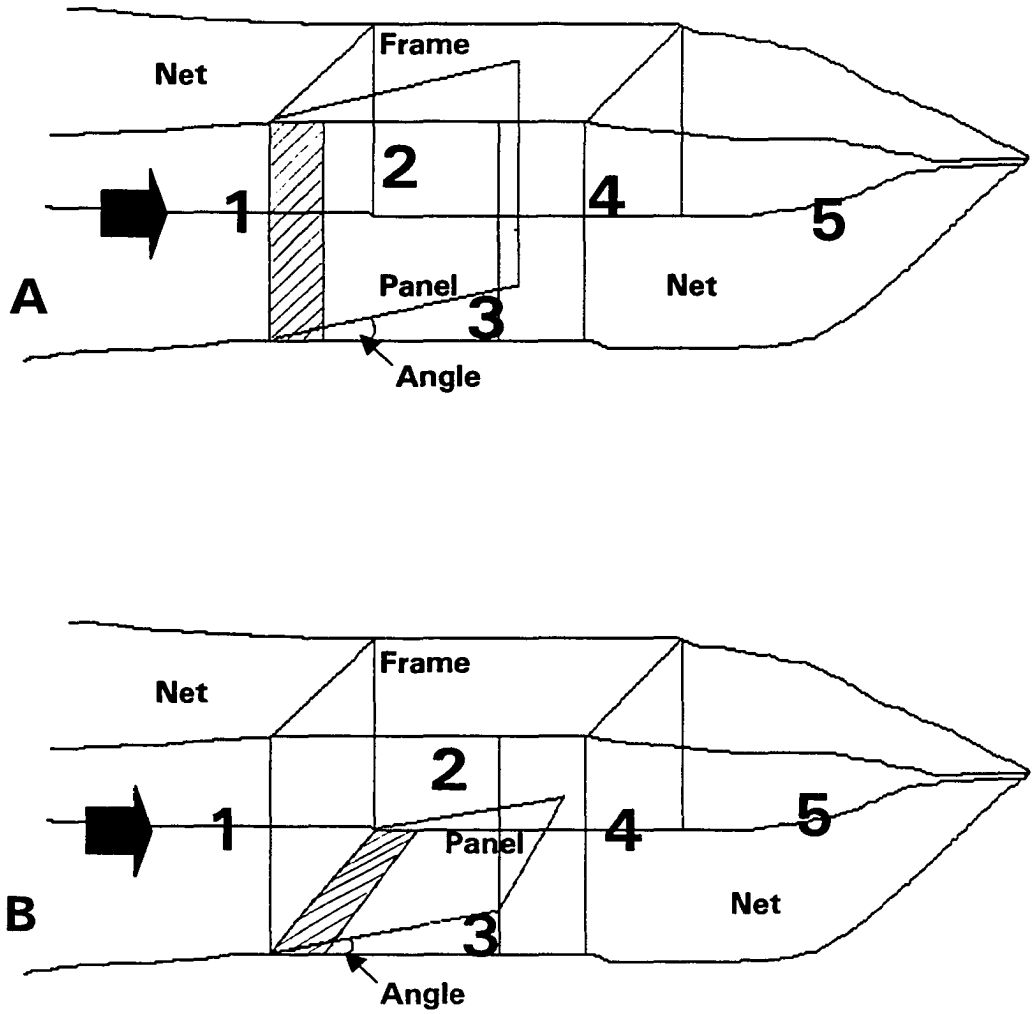


Figure 2.2. Diagram of frame setup for experiments with: (A) vertical and (B) horizontal panel. Numbers indicate locations where snapper positions were recorded: 1 = ahead of the frame, 2 = alongside or above panel, 3 = behind or under panel, 4 = rear of frame, and 5 = behind frame (codend). Arrow refers to the angle at which the panels were set. Escape openings are denoted by hatch marks.

trawl webbing. The frame webbing extended 31 cm behind the frame and was tied closed to simulate a codend. The frame was mounted in the tank so the bottom of the frame was 4 cm above the flume bottom during the vertical panel tests and 6 cm above it when horizontal panels were used. Four vertical and two horizontal panel types were constructed of different materials or webbing configurations

Vertical panels:

(1) **VE15**: 3.5-cm stretch nylon webbing with 15 vertical and 16 horizontal meshes

(2) **VE30**: 3.5-cm stretch nylon webbing with 30 vertical and 16 horizontal meshes

(3) **VESE**: 5-mm nylon seine webbing

(4) **VESO**: 2.25-mm thick Plexiglas sheet with 0.95-cm holes drilled at 5-cm intervals (measured center to center)

Horizontal panels:

(1) **HOME**: 3.5-cm stretch nylon webbing with 11 vertical and 28 horizontal meshes

(2) **HOSO**: 2.25-mm thick Plexiglas sheet with 0.95-cm holes drilled at 5-cm intervals

The VESO and HOSO designs were referred to as solid panels; the remainder were mesh panels. Each panel was hinged to the frame and tested at two angles (vertical, 30° and 45°; horizontal, 10° and 20°). With the 30° angle, the leading edge of the vertical panel was located 23 cm from each side of the frame (the midway point). The 45° angle was the widest setting that would still allow snapper to swim comfortably past the leading edge of the panel, allowing an 8-cm clearance from the frame side. A 10-cm-wide escape opening was located on the side of the

net at the junction with the panel for the vertical panel trials. The horizontal panels were set so the clearance from the panel leading edge to the water surface was either 18 cm (10° angle) or 12 cm (20° angle). The 10-cm-wide horizontal panel escape opening was on the net bottom at the panel junction.

Data Collection

Snapper collected from the holding tanks were gently herded into a net, then carefully transferred to a bucket. Flume water was slowly added to the bucket. Fish were allowed to acclimate in the bucket for at least 15 min before being used in an experiment. The water flow in the flume was increased to the desired velocity before the snapper were released in front of the webbing. A constant water velocity was maintained throughout each experiment. Three one-hour replicates with four snapper per trial were conducted for each of the 12 panel-angle combinations.

The 36 separate experiments (36 hr of observation) were videotaped and later reviewed and scored for data collection. Observational notes were also made while each experiment was in progress. Overt agonistic acts were counted to measure the level of aggression among the snapper. A behavior was considered overt if an individual swam rapidly toward another fish. The second snapper would either maintain position, typically adopting an aggressive posture, or retreat. A long continuous chase was scored as one act. However, if an aggressor stopped, then continued toward the same individual, each approach was considered a separate agonistic act. Snapper that exited the webbed frame, the time of escape, and the number of overt agonistic acts per 5-min interval were recorded. The net was divided into five sections (Figure 2.2), and the number of individuals per section at the end of each 5-min interval was also recorded.

Water velocities (cm/sec) within and around the webbing-covered frame were measured with a Global Flow Probe Model FP101 (Global Water Instrumentation, Fair Oaks, CA). Twenty measurements were averaged at each location. The standard deviation of these measurements was used as an index for turbulence.

Data Analysis

Prior to accepting an analysis of variance model, residuals were examined for univariate normality and homogeneity of variances. Normality was assessed with the W-statistic developed by Shapiro and Wilk (1965). A modified Levene test was used to test for homogeneity of variances. The results indicated the raw data were not distributed normally and variances were nonhomogeneous. The number of agonistic acts per 5-min interval were transformed by ln(acts + 1), square root(acts + 1), or reciprocal(acts + 1). These transformations were used in an effort to create a new variable which met the criteria of being approximately normally distributed with homogeneous variances. The ranked number of agonistic acts was also compared in a nonparametric analysis of variance (ANOVA) model. None of the transformed variables met both the normality and homogeneous variance assumptions. However, the log-transformed residuals were normally distributed. Although the Levene's test indicated that the variances were not homogeneous, in all cases, the results of the ANOVA on the log-transformed variable were very similar to those of the nonparametric ANOVA (on ranked data). The log-transformed variable was used in analyses instead of the nonparametric test because of the availability of post-ANOVA procedures. When differences were found, the means were examined, and the Tukey procedure for pairwise comparisons was used to determine the nature of these differences (Neter et al. 1990). Statistical analysis was performed with the SAS/STAT Software for Windows, Version 6.12 (SAS Institute, Inc., Cary NC).

Data from the panel experiments were analyzed with the model: log (agonistic acts + 1) = panel, angle, time, and the interactions of these terms. A separate analysis was conducted for each panel orientation. Vertical panels were VE15, VE30, VESE, and VESO and angles were 30° and 45°. Horizontal panels were HOME and HOSO and angles were 10° and 20°. Each one-hour replicate was divided into three equal time periods (early, mid, and late).

Field Observations

Behavior of juvenile red snapper in shrimp trawls was examined from numerous videotapes recorded by NMFS divers at the Harvesting Systems Branch in Pascagoula, MS. Snapper behavior in trawls was also discussed with several of the NMFS divers stationed at the Pascagoula Facility.

Results

Water Velocities

Mean water velocities for the various panel and angle combinations are illustrated in Figures 2.3 through 2.9. In general, the panels decreased water velocities, although the degree of reduction depended on the panel material and configuration. Velocity reductions from least to greatest were VE15<VE30<VESE<VESO for the vertical panels and HOME<HOSO for the horizontal panels. The solid panels had the greatest decrease, creating a reduced-flow area behind them where flows were less than 5 cm/sec. The size of this area depended on the angle at which the panel was set; wider angles created larger reduced-flow areas. Velocities, and occasionally turbulence, of the water flowing alongside (or over) the panels, particularly the solid type, typically were higher. The horizontal panels had the largest area of reduced flow behind them.

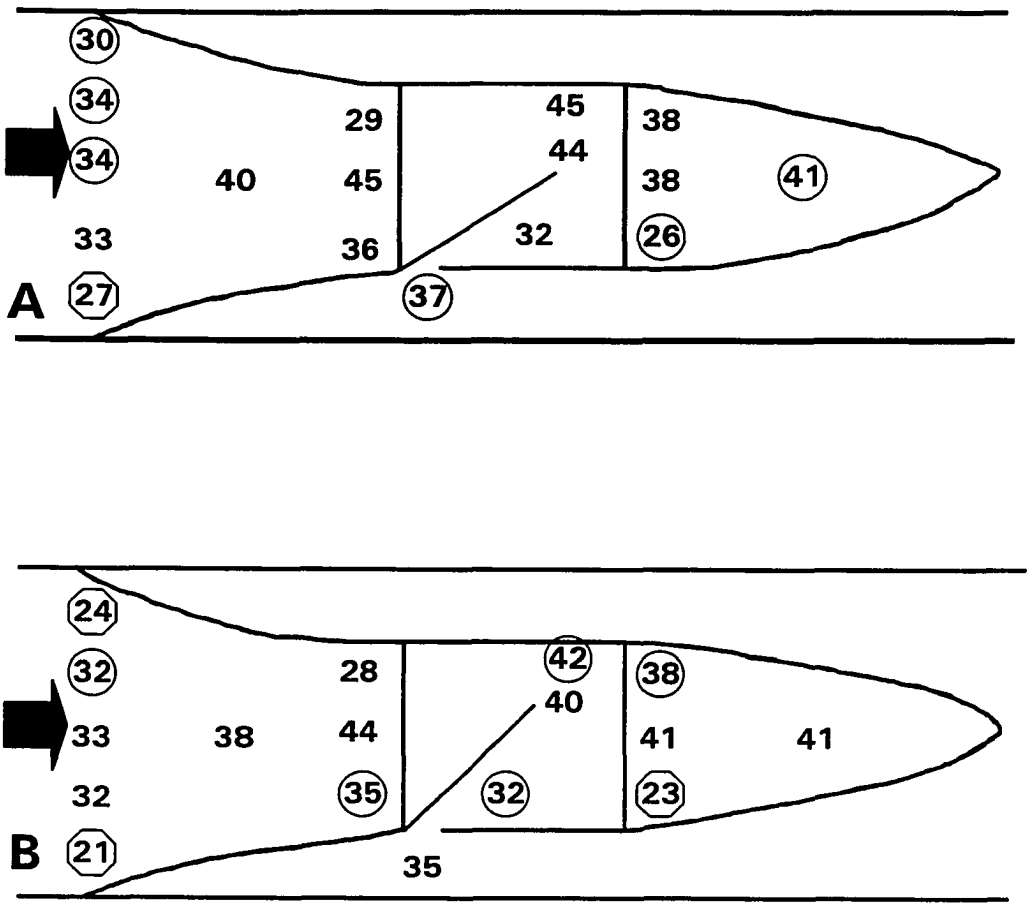


Figure 2.3. Top view of vertical-panel setup. Numbers are mean water velocities (cm/sec) for the VE15 panel set at: (A) 30° and (B) 45°. An index of turbulence, as measured by the percentage of the standard deviation divided by the mean, is indicated by the symbols: none (index≤2%), circle (2<index≤4%), square (4%<index<10%), and octagon (index≥10%).

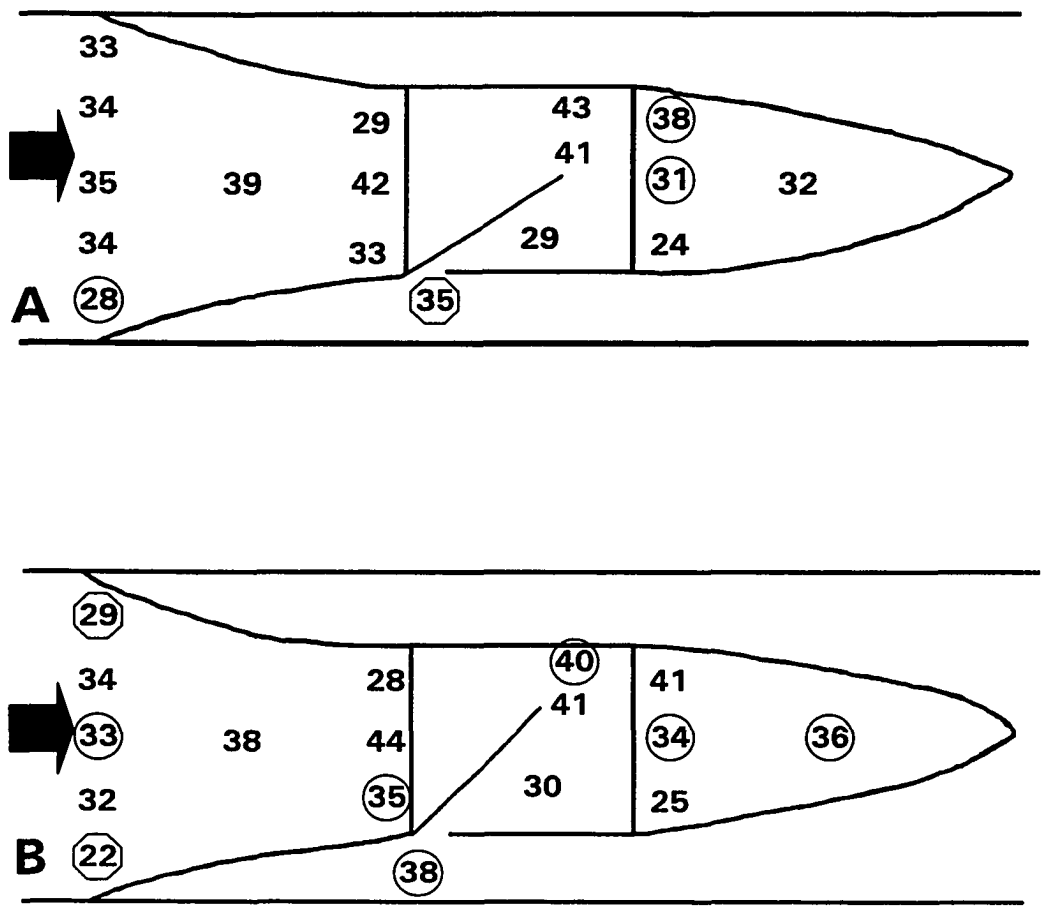


Figure 2.4. Top view of vertical-panel setup. Numbers are mean water velocities (cm/sec) for the VE30 panel set at: (A)30° and (B) 45°. An index of turbulence, as measured by the percentage of the standard deviation divided by the mean, is indicated by the symbols: none (index≤2%), circle (2<index≤4%), square (4%<index<10%), and octagon (index≥10%).

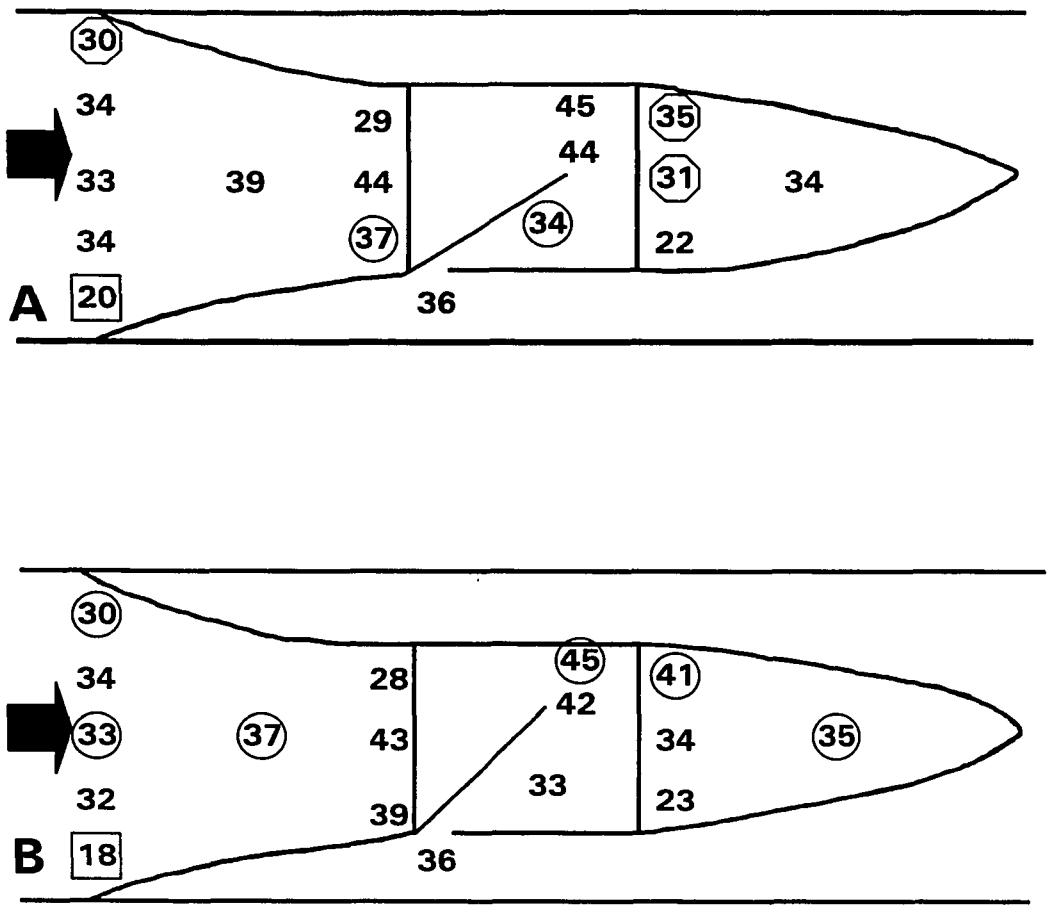


Figure 2.5. Top view of vertical-panel setup. Numbers are mean water velocities (cm/sec) for the VESE panel set at: (A) 30° and (B) 45°. An index of turbulence, as measured by the percentage of the standard deviation divided by the mean, is indicated by the symbols: none (index≤2%), circle (2<index≤4%), square (4%<index<10%), and octagon (index≥10%).

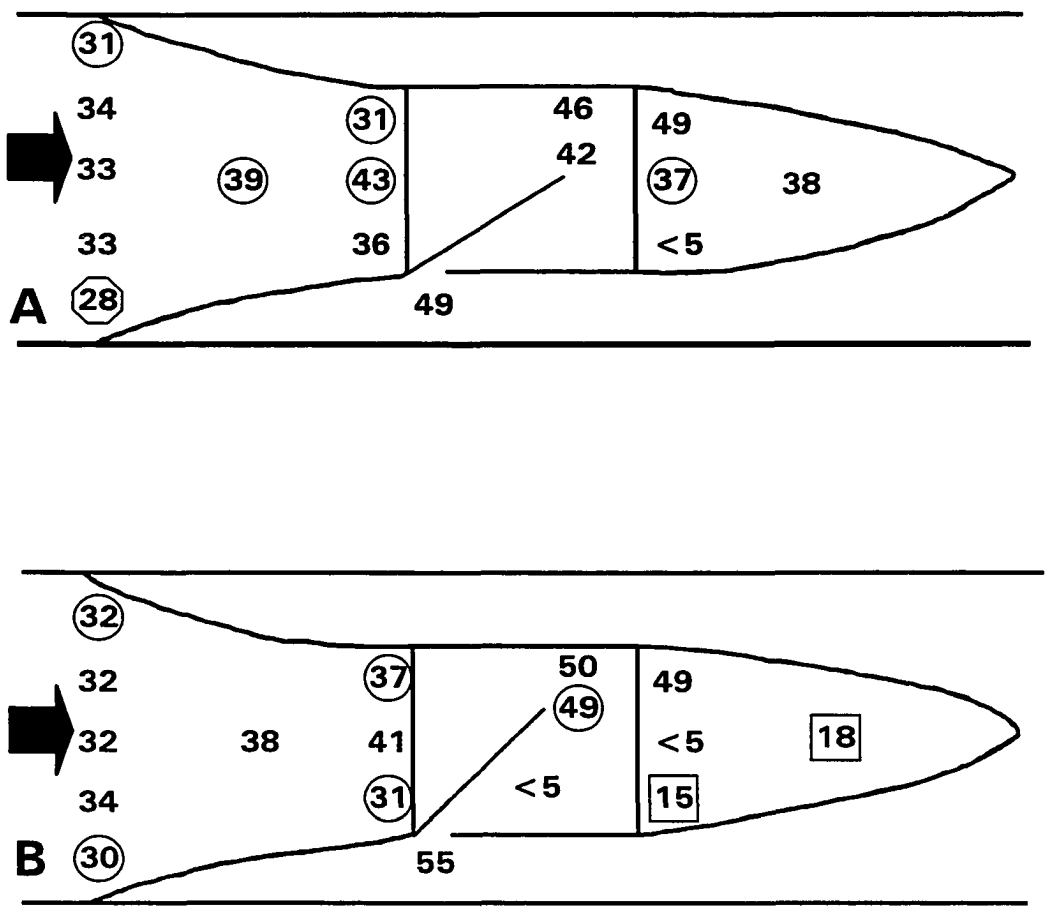


Figure 2.6. Top view of vertical-panel setup. Numbers are mean water velocities (cm/sec) for the VESO panel set at: (A) 30° and (B) 45°. An index of turbulence, as measured by the percentage of the standard deviation divided by the mean, is indicated by the symbols: none (index≤2%), circle (2<index≤4%), square (4%<index<10%), and octagon (index≥10%).

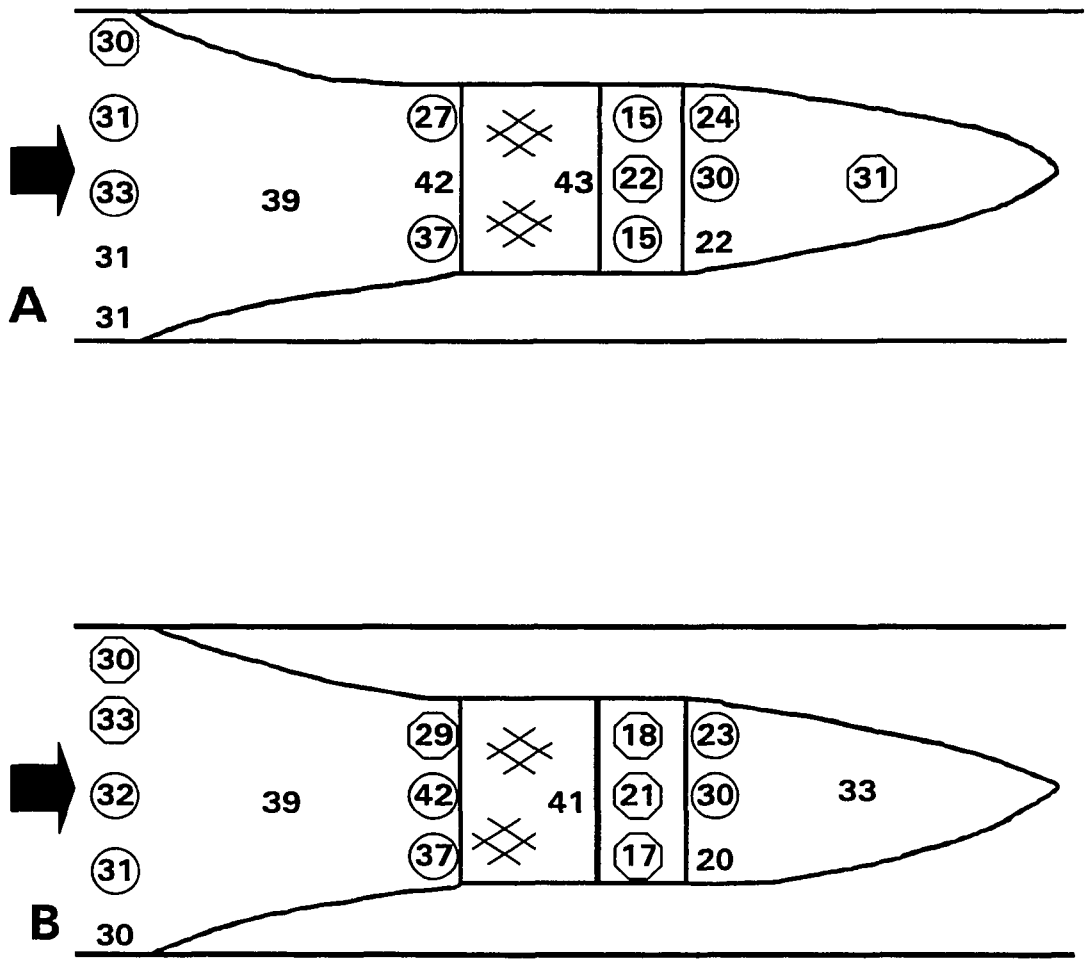


Figure 2.7. Top view of horizontal-panel setup. Numbers are mean water velocities (cm/sec) for the HOME panel set at: (A) 10° and (B) 20°. An index of turbulence, as measured by the percentage of the standard deviation divided by the mean, is indicated by the symbols: none (index≤2%), circle (2<index≤4%), square (4%<index<10%), and octagon (index≥10%).

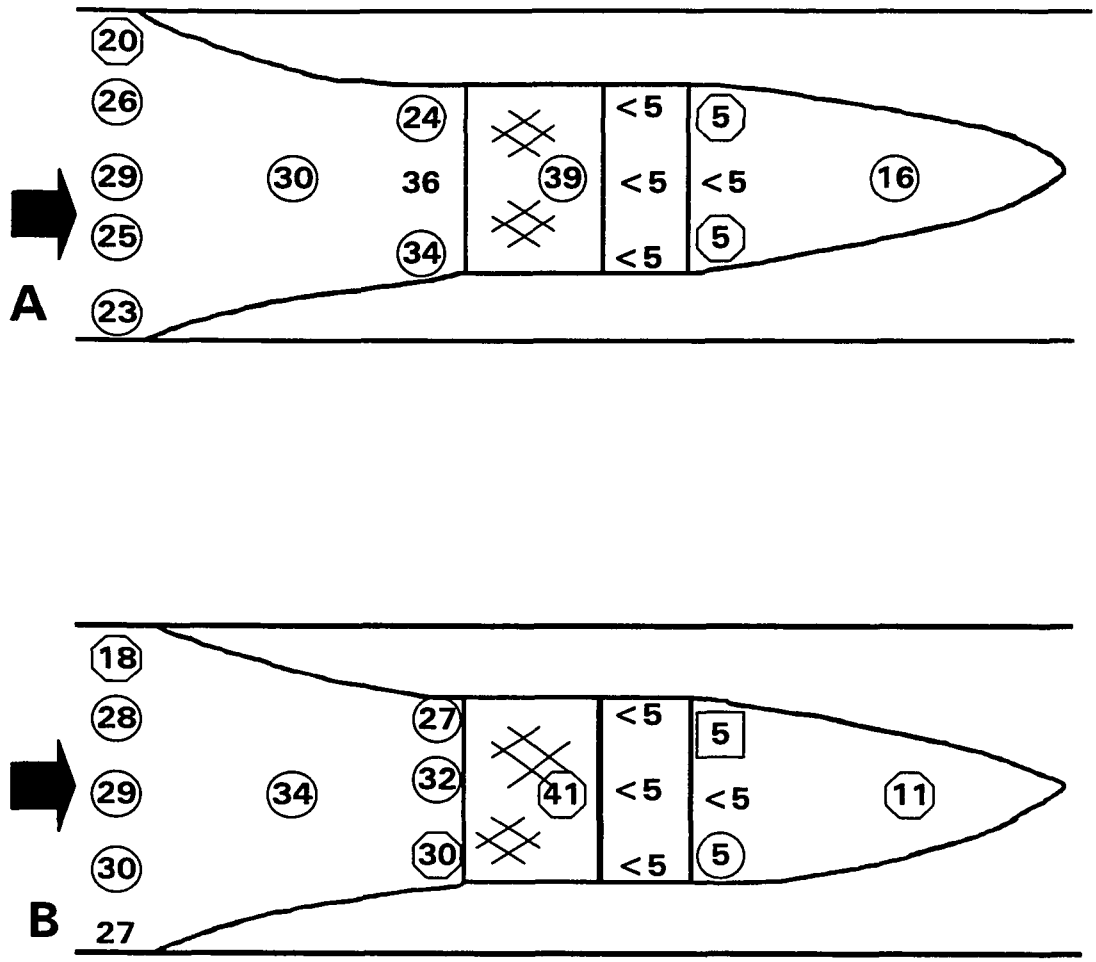


Figure 2.8. Top view of horizontal-panel setup. Numbers are mean water velocities (cm/sec) for the HOSO panel set at: (A) 10° and (B) 20°. An index of turbulence, as measured by the percentage of the standard deviation divided by the mean, is indicated by the symbols: none (index≤2%), circle (2<index≤4%), square (4%<index<10%), and octagon (index≥10%).

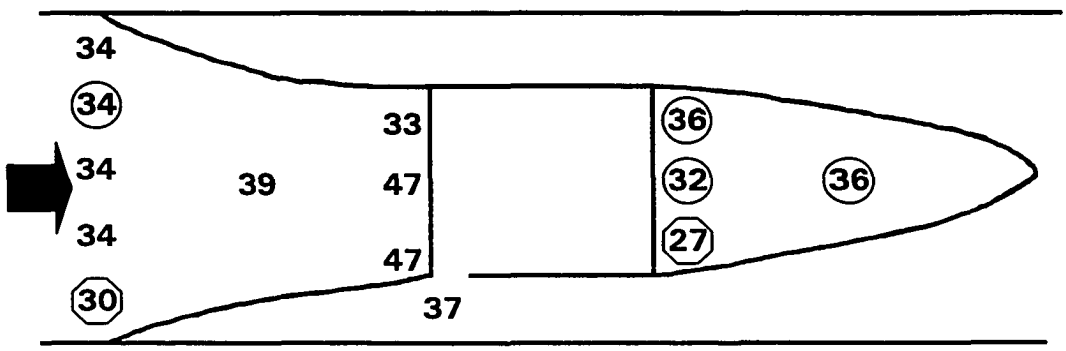


Figure 2.9. Top view of setup with no panel. Numbers are mean water velocities (cm/sec). An index of turbulence, as measured by the percentage of the standard deviation divided by the mean, is indicated by the symbols: none (index≤2%), circle (2<index≤4%), square (4%<index<10%), and octagon (index≥10%).

General Observations

The snapper tended to remain near the bottom in the current. When the flume was turned off, the fish often aggregated, moved forward, and swam higher in the water column. Smaller snapper were forced into the codend more frequently than larger individuals. Fish that were pushed to the back of the codend displayed little agonistic behavior and distances between the snapper were often quite small. These snapper would drift back until their tails touched the webbing at the back of the codend, then swim forward. This behavior was repeated frequently unless an individual became fatigued and was unable to swim against the current.

Within the frame, there appeared to be a certain distance at which snapper in lower flow areas would allow other individuals to remain before initiating an agonistic attack. As an experiment progressed, this distance shortened. Frequently, individuals that were attacked would be forced near other snapper that would subsequently become aggressive.

Agonistic behavior was typically preceded by an aggressor assuming a head-down posture with pectoral and pelvic fins spread out and dorsal fin erect. A tired snapper would often angle its head up and tilt its body toward one side instead of remaining vertical. Very tired individuals would lie on the bottom of the net with a lateral bend in the caudal region until they recovered.

Vertical Panels

A total of 96 snapper were used in the vertical panel experiments. Four of the five escapes occurred during the replicates with solid panels (Table 2.1). Analysis of variance on the vertical panel agonistic activity data indicated there was a significant panel-angle interaction ($P > F = 0.001$ - Table 2.2). The mean level of agonistic behavior with the 45° angle was higher than that of the 30° angle for the VE30 and

Table 2.1. Fish escapes during panel experiments. Fish that went back into the net through the escape opening are also recorded. *Denotes pushed out by other fish.

Panel	Angle	Replicate	Number of fish (minutes into experiment that fish exited)
Vertical panels:			
VE15	45°	3	1 (0:21)
VESO	30°	1	1 (0:05)*
		2	1 (0:24)
	45°	3	1 (0:10)*; 1(0:31)*
Horizontal panels:			
HOME	10°	3	1 (0:21)
	20°	3	1 (0:02); 1 (0:24)
HOSO	10°	1	1 (0:09), back in at 0:16 for remainder
		2	1 (0:05)
		3	1 (0:24)
	20°	1	1 (0:14)*; 1 (0:19)
		2	1 out then in (0:13), 1 out*(0:14), other out (0:15), both in (0:15), 1 out then in (0:27), 1 out then in (0:44), 1 out then in (0:58)
		3	1 out then in (0:05), 1 out*(0:10), 1 out (0:10), 1 in (0:21), 2 out (0:23), 1 in (0:23), 3 fish in and out

Table 2.2. Results of analysis of variance for log (agonistic acts + 1) during the vertical panel experiments. Panels were: VE15, VE30, VESE, and VESO. Angles were: 30° and 45°. Times were: early (<20 min), mid (20-40 min), and late (40-60 min).

Source	DF	Mean Square	F-value	Pr>F
Panel	3	3.20	4.99	<0.01
Angle	1	7.90	12.35	<0.01
Panel*Angle	3	8.40	13.13	<0.01
Time	2	1.64	2.56	0.08
Panel*Time	6	1.10	1.73	0.12
Angle*Time	2	0.51	0.80	0.45
Panel*Angle*Time	6	0.51	0.80	0.57
Error	264	0.64		
Corrected Total	287			

VESE panels (Figure 2.10). In contrast, the mean number of agonistic acts for the VE15 and VESO panels was slightly lower, or nearly the same, when the angle was set at 45° than at a 30° angle.

The percent of snapper found in each of the five sections denoted in Figure 2.2 is given, by panel type and angle, in Figures 2.11 through 2.14. The agonistic behavior affected fish positioning around the panel and made it difficult to discern trends. The positions of the fish may not truly reflect preference but merely indicate the location to which an individual was chased by other snapper. Only on rare occasions did more than one snapper stay behind a panel (Section 3). The snapper tended to remain in front of, or behind, the frame when the VE15 panel was set at 30°(Figure 2.11). Few fish got behind the panel at this setting. The snapper were somewhat evenly distributed among the first four sections when this panel was set at 45°, and tended to be behind the panel (Section 3) more frequently than with the panel set at 30°. When the VE30 panel was set at 30°, snapper were more often in the codend or behind the panel (Figure 2.12). When this panel was set at 45°, snapper were either in front of, or behind the frame, and few were behind the panel. Few snapper got behind the VESE panel set at either angle (Figure 2.13). The snapper were mainly in the back of the frame, or behind it. When the VESO panel was used, the snapper tended to stay behind the frame (Figure 2.14) at either angle, although at 45°, several fish were alongside the panel (Section 2).

Horizontal Panels

A total of 48 snapper were used in horizontal panel experiments. Twelve of the 15 escapes occurred during the solid-panel replicates (Table 2.1). However, five of the individuals that escaped during the horizontal-solid-panel experiments went back through the escape opening into the net. There was a significant interaction between

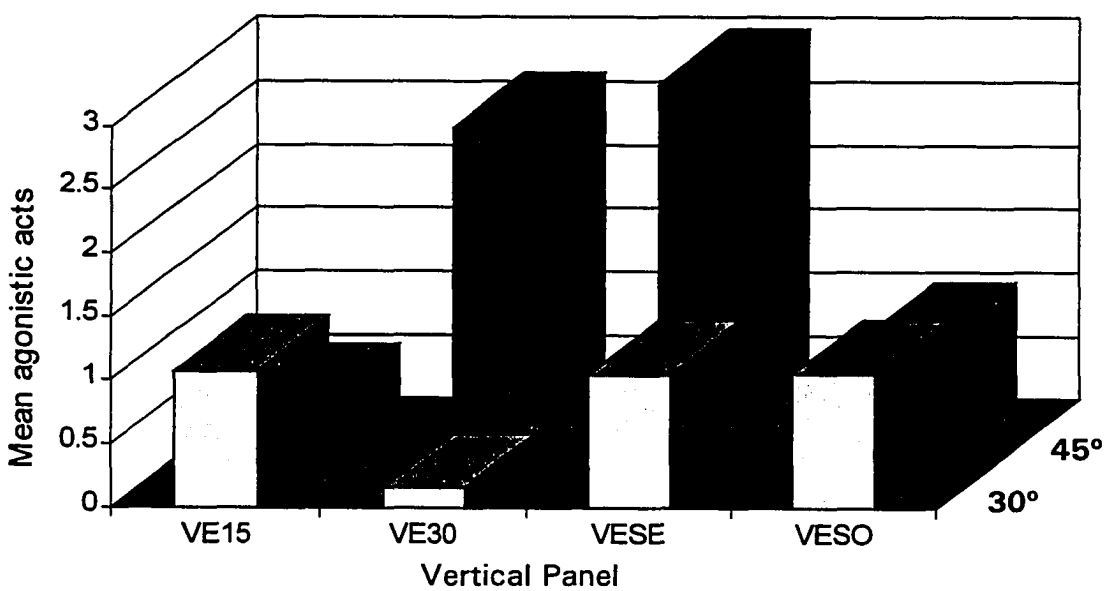


Figure 2.10. Mean number of overt agonistic acts, by panel type and angle, for vertical panel experiments.

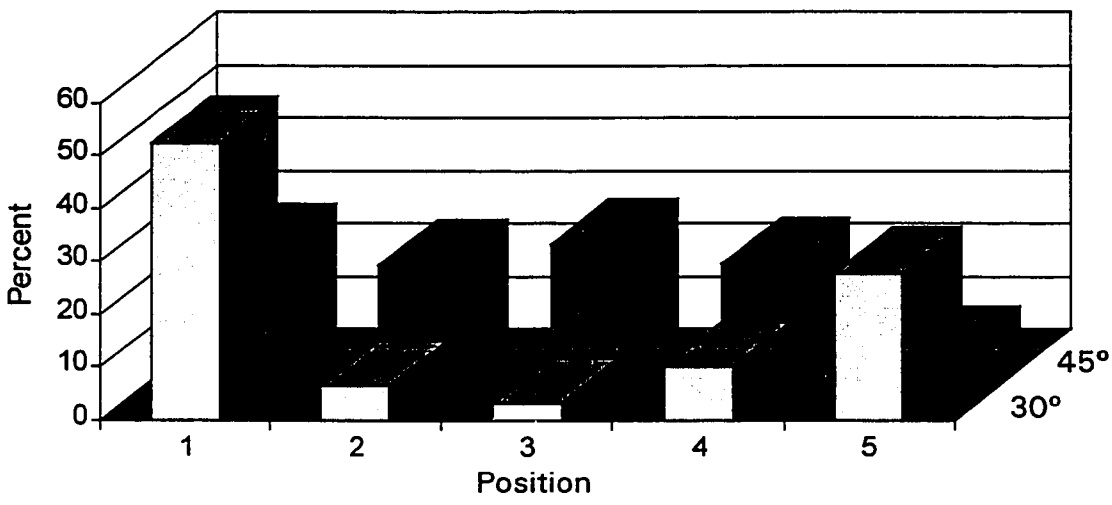


Figure 2.11. Mean percentage of snapper in each of the five sections denoted in Figure 2.2 for the VE15 panel, by angle. Section 3 is behind the panel.

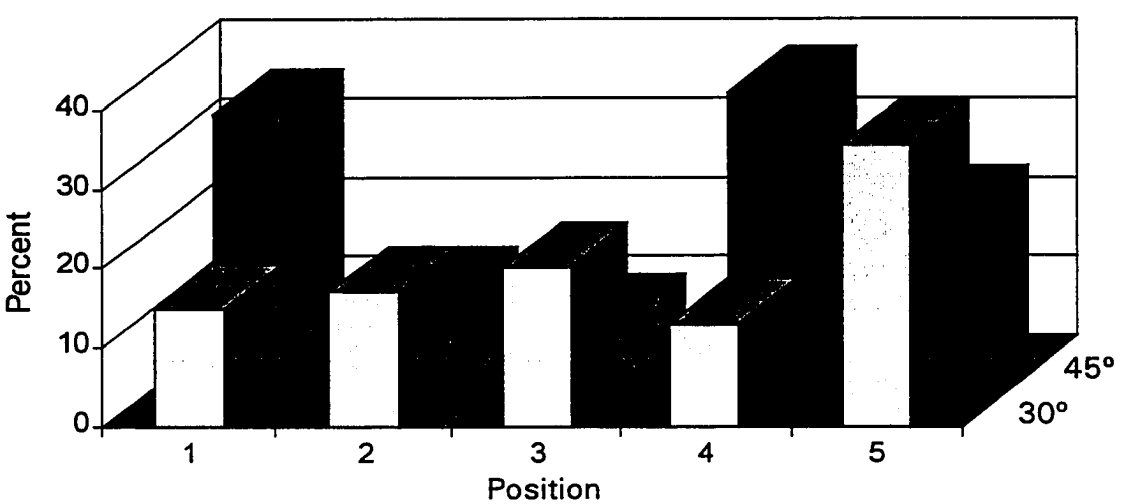


Figure 2.12. Mean percentage of snapper in each of the five sections denoted in Figure 2.2 for the VE30 panel, by angle. Section 3 is behind the panel.

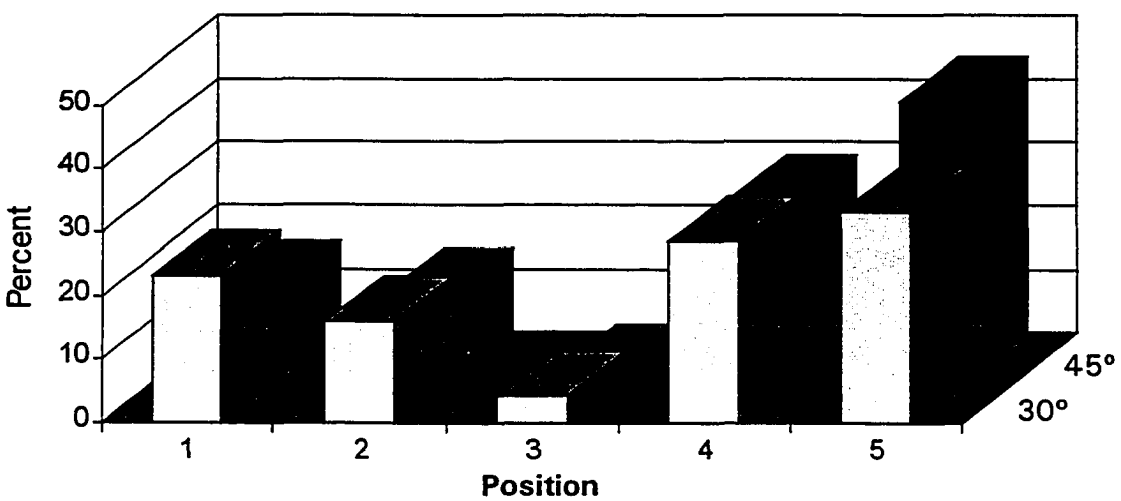


Figure 2.13. Mean percentage of snapper in each of the five sections denoted in Figure 2.2 for the VESE panel, by angle. Section 3 is behind the panel.

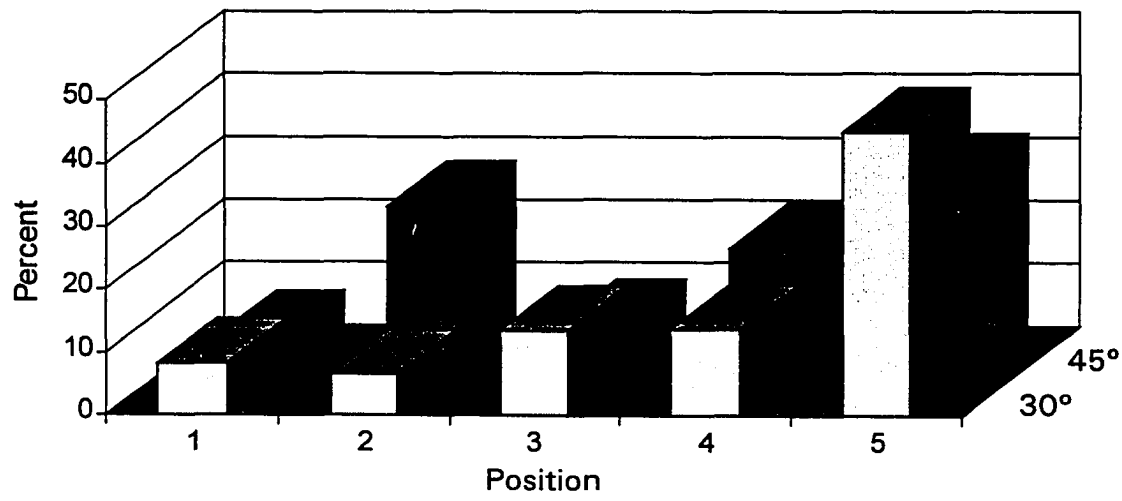


Figure 2.14. Mean percentage of snapper in each of the five sections denoted in Figure 2.2 for the VESO panel, by angle. Section 3 is behind the panel.

panel type and time in the horizontal-panel analysis ($P>F=0.04$ - Table 2.3). This interaction occurred because agonistic behavior was higher with the solid panels during the first 20 min, whereas there was little difference late in the experiment (Figure 2.15).

The percent of snapper found in each of the five sections denoted in Figure 2.2 is given, by panel type and angle, in Figures 2.16 and 2.17. With the HOME panel, the snapper tended to stay in front of the frame, although several were in the codend with the panel set at 10° (Figure 2.16). With the HOSO panel at either angle, the fish either stayed in front of the frame, under the panel, or in the codend (Figure 2.17).

Preliminary and Additional Panel Experiments

Observations of red snapper behavior were made during preliminary testing to examine factors that could potentially affect behavior such as the presence of external stimuli and fish density. These initial experiments were conducted before the actual testing occurred to suggest methods to eliminate potential sources of variability in the data. The tank setup and testing protocols were altered based on the results of these experiments. Additional experiments were designed to examine effects of vertical rods versus square tubing, artificial decoys, and the presence of one-year-old fish on the behavior of juvenile snapper.

Trials without black felt

To observe whether snapper behavior may be affected by the artificial environment, several snapper were placed into the flume tank without current. The snapper remained along the inside edge of the flume. The Plexiglas transmitted light very strongly and was transparent to outside activity. Black visqueen was initially used to cover the sides of the tank to provide a background for videotaping and to reduce sources of light and potential distractions because of movements of paddles

Table 2.3. Results of analysis of variance for log (agonistic acts + 1) during the horizontal panel experiments. Panels were: HOME and HOSO. Angles were: 10° and 20°. Times were: early (< 20 min), mid (20-40 min), and late (40-60 min).

Source	DF	Mean Square	F-value	Pr > F
Panel	1	4.40	12.17	<0.01
Angle	1	0.18	0.50	0.48
Panel*Angle	2	0.48	1.33	0.25
Time	2	3.78	10.48	<0.01
Panel*Time	2	1.16	3.23	0.04
Angle*Time	2	0.50	1.38	0.26
Panel*Angle*Time	2	0.13	0.37	0.69
Error	132	0.36		
Corrected Total	143			

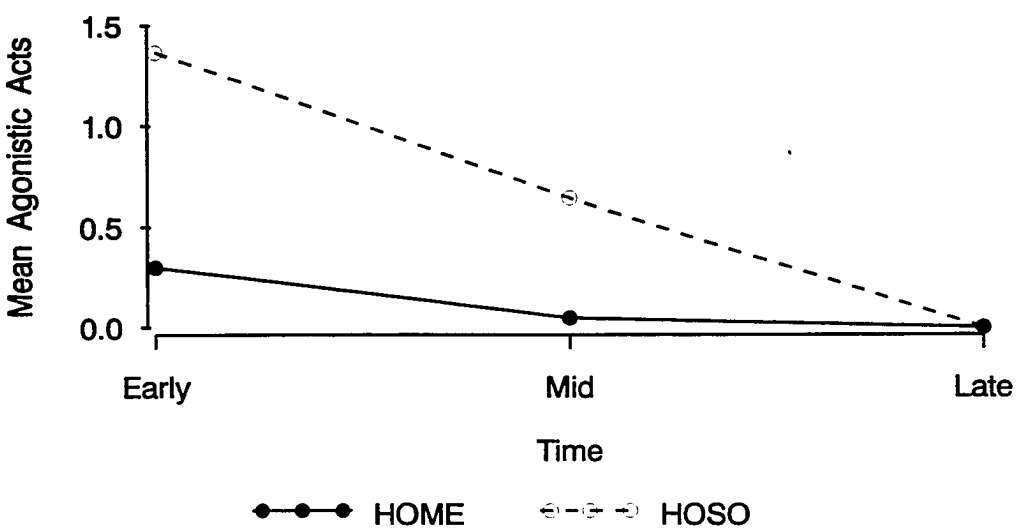


Figure 2.15. Mean number of overt agonistic acts by panel type and angle for horizontal panel experiments.

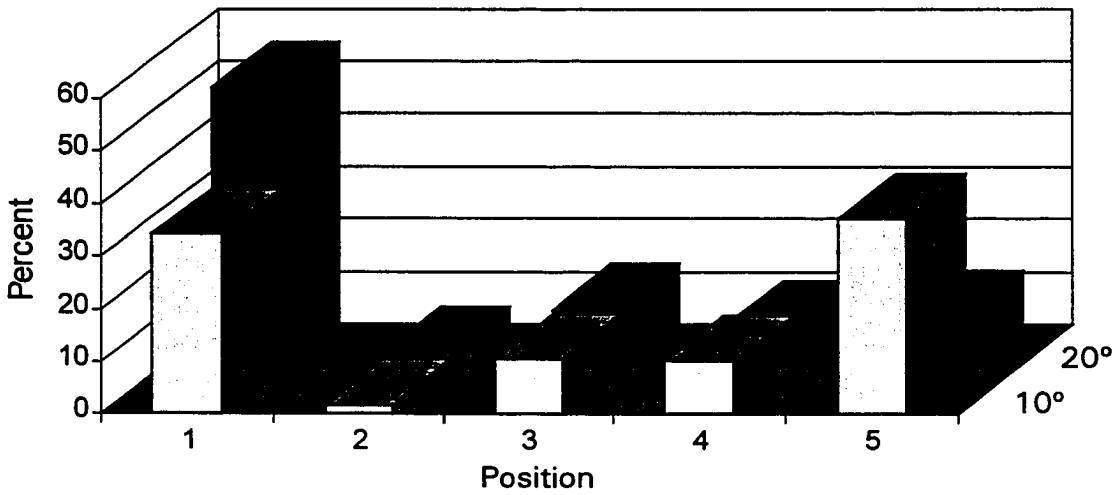


Figure 2.16. Mean percentage of snapper in each of the five sections denoted in Figure 2.2 for the HOME panel, by angle. Section 3 is under the panel.

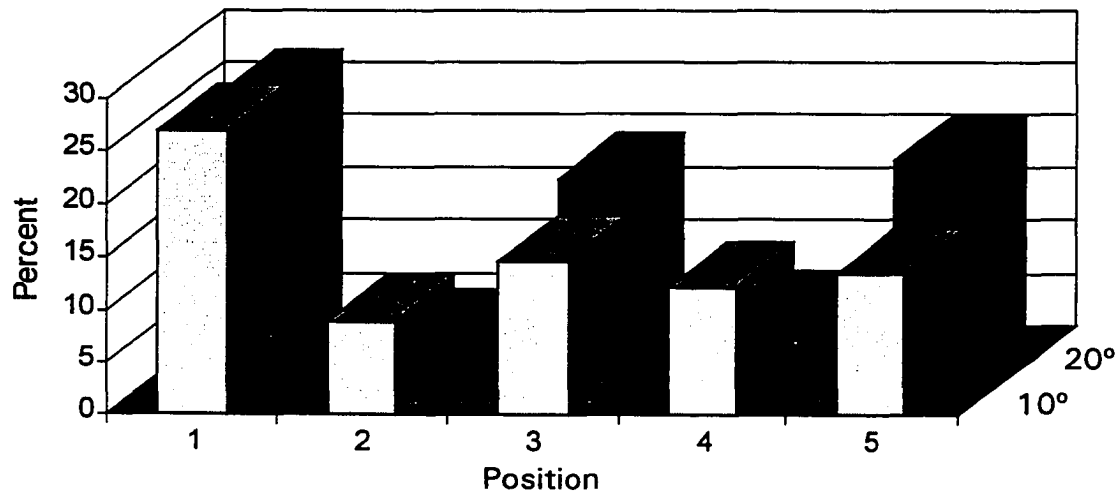


Figure 2.17. Mean percentage of snapper in each of the five sections denoted in Figure 2.2 for the HOSO panel, by angle. Section 3 is under the panel.

and personnel. The visqueen did not reduce the time the snapper spent near the walls, and the fish actually appeared to swim along the wall more frequently. The surface of the visqueen was very shiny, and the snapper may have observed their reflections in the glass. When the sides and bottom of the tank were covered with black felt, the fish explored all parts of the flume working channel.

Single and paired fish trials

To examine the potential influence on their behavior of the number of snapper present in the flume, preliminary trials without flow were conducted with one, two, three, and four snapper. Single fish would either swim to a corner of the tank and remain there, or dart about erratically. Pairs of snapper swam less erratically and spent more time exploring the tank. When three or four fish were placed in the tank, the fish explored the flume thoroughly. Because the unusual behavior displayed by single or paired fish could have potentially affected the results, at least three snapper were used in all experiments.

Trials without codend around the frame

Initial trials with flow conducted with fine-mesh webbing on the panel and the rest of the frame uncovered met with little success. The snapper did not stay around the frame and ended up against the backstop. The frame was then surrounded by the codend from a 6-m headrope length trawl to restrict the snapper to a more confined area.

Vertical panel with fine webbing

A 28- by 28-mesh panel constructed of very fine (0.6 mm diameter) twine 1.8-cm-stretch mesh webbing was used during the initial vertical-panel trials. The snapper did not get behind the fine-mesh-webbing panel during the tests, and water velocity measurements indicated that the panel did not perceptibly slow the water

flow. During these tests, most snapper were swept quickly into the codend. Subsequent trials were conducted with webbing panels with thicker (1.5-mm diameter) twine (VE15), more meshes (VE30), smaller meshes (VESE) and a solid panel (VESO) to create various reductions in water flow.

Vertical rods and tubing

Several different types of vertical rods and tubing were placed in front of the frame to examine whether snapper preferred to get behind the larger bars or if the turbulence created by the square tubing would attract snapper more than pipe. Vertical rod and tubing types tested included:

(1) 0.95-cm diameter rods spaced 10.8 cm apart

(2) alternating 1.9-cm diameter pipe and square tubing spaced 8.26 cm apart.

The snapper occasionally got behind the small rods, but spent little time there; one snapper got behind one of the small diameter rods for 2.5 min. During one trial, two snapper got behind the square tubing while one individual was behind the 1.9-cm pipe. During a subsequent trial, two fish got behind the 1.9-cm pipe while one fish was behind the square tubing. However, during the panel experiments, the snapper frequently swam behind the small-diameter vertical bar at the end of the webbing panel.

The snapper in these experiments appeared to prefer vertical bars that were associated with webbing, rather than those that were not. There did not appear to be a difference in snapper preference between square and round tubing.

Fish decoys

Snapper behavior was observed in the presence of five different fishing lures (with hooks removed), including a 6.5 cm Poes Lures (Morgan, UT) model RC1 Series 1900, an 8-cm Bagley Bait Co./Firehawk Fishing Lure Manuf. Co. (Winter Haven, FL)

model DB3, an 18-cm 18 SM MAG Silver Mackerel Floating Lure by Rapala, OY (Finland), an 18-cm 18 GFR MAG Gold Fluorescent Red Floating Lure by Rapala, OY (Finland), and an 18 cm long and 5 cm high red-orange Giant Trembler T190-213 by Seven Strand (Long Beach, CA). Different lures were selected to be either: a similar size and color, similar size and different color, larger size and similar color, or larger size and different color than the snapper. The lures were suspended from monofilament fishing line into the webbing-covered frame with the panel completely open (tied to the side of the frame). Lures were either suspended near the snapper or manually manipulated toward the fish.

The small lures had no effect on the position or behavior of the snapper. Larger lures only affected fish position when they were quickly moved and the fish moved away from the lure. When lures were stationary or slowly moved, the snapper often swam alongside the lure or drafted behind it.

Trials with 1-year-old snapper

I hypothesized that larger snapper would be better able to swim against the current and that their presence would improve escapement by reducing the number of agonistic acts among the young-of-the-year red snapper. During three trials, 180- and 190-mm snapper were placed into flume with four juvenile snapper. The larger snapper rarely moved from the bottom of the net, regardless of velocity. The presence of larger snapper did not affect the positioning of the smaller snapper. On several occasions, the smaller snapper actually swam behind the larger snapper and remained in the area of reduced water flow behind the larger fish.

Discussion

Effectiveness of Panels

Many of the snapper that exited the horizontal panel opening came back into the net through the same opening. This behavior has also been observed in juvenile snapper exiting BRD's in trawls (Workman et al. 1998a). Most of the snapper in the laboratory escaped when panels set up low-flow areas where flows were less than 10 cm/sec. Workman and Foster (1994) suggested that 20 to 50 cm/sec was a good release velocity. In field observations, at velocities less than 20 cm/sec, fishes in trawls tended to swim in circles. The snapper in the laboratory defending the low-flow area behind the panels would frequently turn around to face other snapper attempting to enter the low-flow area. A similar phenomenon was observed during trawling (I. Workman, NMFS Pascagoula Laboratories, personal communication) where fishes would turn around in some BRD's. However, reverse flows were measured behind these devices, whereas reverse flows were not detectable in the laboratory.

The snapper in the laboratory appeared to allow other individuals to get within a certain distance before they initiated agonistic activity. This distance became shorter as the fish became fatigued. Another possibility is that the snapper in the laboratory were defending the area immediately around them, instead of a fixed-area territory. 'Personal space' defense was also observed in the bay goby, *Lepidogobius lepidus* (Grossman 1980). The snapper in the laboratory generally stopped whatever they were doing to watch laboratory personnel. The flume was covered with black felt to reduce effects of outside activities on fish behavior. The high level of agonistic activity observed in the laboratory could be due in part to confinement of the snapper, although the snapper were selected randomly from the tanks in an effort

to reduce that possibility. Also unknown is the effect of high turbidity or darkness on agonistic behavior. Agonistic behavior appears to be primarily visual and would likely be reduced, or not occur, under these conditions.

Divers have observed overt agonistic behavior in juvenile snapper in shrimp trawls. A larger juvenile was observed chasing not only smaller snapper, but also fish closer to its size, from the area near a BRD escape opening (I. Workman, NMFS Pascagoula Laboratories, personal communication). Agonistic behavior was also observed in several of the NMFS videos. However, based on these videos and diver observations, agonism does not appear to occur as frequently in trawls as was observed in these laboratory experiments. Snapper in the trawls were frequently observed in closer proximity without aggression than those fish in the laboratory experiments. However, based on the frequency of tailbeats, the snapper in the NMFS videos were swimming faster than those fish in the laboratory. Lack of reduced-flow areas or velocities higher than those used in the laboratory may also reduce agonism because fishes are tired. Ferguson et al. (1983) found that juvenile lake charr, *Salvelinus namaycush*, spent more time near the bottom and moved about less under higher velocities; however, velocity had no effect on agonistic behavior patterns. In contrast, aggression of juvenile Atlantic salmon, *Salmo salar*, and brook trout, *Salvelinus fontinalis*, decreased when water flows were less than 5 cm/s because fishes tended to hide in the substrate (Gibson 1978). Other factors could potentially reduce agonistic behavior among juvenile red snapper in trawls. The presence of predatory fishes may reduce agonism, although the use of TED's should reduce the number of larger fishes caught in trawls. Other nonpredatory species may reduce agonism because of crowding. Divers are frequently used to videotape fishes in trawls; their presence may also reduce agonistic behavior. During the dives, the

snapper did not generally move away from the divers, except when they attempted to evade capture.

It appears that the behavior of juvenile snapper in shrimp trawls is a complex interaction between water velocities, stamina and swimming ability of the snapper, and the presence of desirable low-flow areas. If low-flow areas are absent, aggression will likely be absent or reduced. When water velocities are high, individuals either have to swim or fall back to the codend, and there is little opportunity for aggression. Lower velocities with or without low-flow areas create the opportunity and impetus for aggression to occur.

More research is needed on basic behavior of fishes in addition to the complex responses of each species to fishing gears in order to reduce bycatch. Work is especially needed to identify which factors will stimulate fishes to leave nets and, if possible, to determine the limits beyond which selectivity is lost (Wickham and Watson 1976).

Fish Behavior in Trawls

Fishing gear is designed to make fishes behave maladaptively (Fernö 1993). A trawl is not a simple stimulus but a complex assemblage of optical and acoustic stimuli that originate in different parts of the gear (Hemmings 1969). The process of the fish capture by a fishing gear involves interactions between physical aspects of the gear and behavioral aspects of the fish species involved (Parrish 1969). Species differ in their response to trawls (Okonski 1969; Wardle 1993). Vyskrebentsev (1968) distinguished three main groups of fishes according to their reaction to gear: (1) bottom, nonschooling species where near orientation determines behavior around gears and no fright response is seen; (2) pelagic species, scattered in small, sparse schools where preliminary activation and mobilization of receptor sensitivity occurs

prior to contact with the gear, do not display a fright response and often turn towards the trawl or cables; and (3) typically schooling species, that meet the gear in large aggregations and sense the gear at a distance, long before visual contact is established. Variations in responses to fishing gears can be explained as a trade off between different factors, for example, reproductive state or presence of prey (Fernö 1993). Larger schools may display a weaker response to fishing gears since they will react to a predator at a longer distance but a lower intensity. Differences in behavior between fishes of different sizes is probably not only a function of swimming ability or mesh sorting, but could be because of differences in reaction distance (Fernö 1993).

Fishes display two basic reactions to moving gears such as trawls. Initially, they maintain station with the net or its parts (Wardle 1983). Some larger species, such as Atlantic cod, *Gadus morhua,* and haddock, *Melanogrammus aeglifinus*, can swim in the mouth of trawls for extended periods (Wardle 1993). Individuals then turn and allow the gear to pass around them (Aronov and Vyskrebentzev 1969; Wardle 1983). Juvenile red snapper generally do little to avoid an approaching trawl; most snapper rise up over the footrope and enter the net (Watson et al. 1992). Within the net, snapper avoid contact with the webbing and go into the codend. Although most trawls in the Gulf of Mexico are towed at speeds of around 2 to 3 knots (1 to 1.5 m/s), velocities within the trawls are typically slower. In the codend, where water flows are generally slower (High 1969; Watson 1988), snapper orient into the direction of water flow and appear to exhibit an optomotor response (Workman and Foster 1994). The juvenile snapper in the flume also oriented into the current. When objects, such as BRD's or debris, are in a trawl, juvenile fishes position themselves in the slower turbulent flow behind an object (Watson et al.

1992). Although the snapper in this study got behind the panels, aggressive behavior by one snapper would prevent other individuals from occupying the same area of reduced-water flow.

The optomotor reaction appears to play an important role in the behavior of fishes in relation to trawls. In a full optomotor reaction, individuals get a visual fix on, and swim parallel to, a moving background, such as a section of a trawl (Arnold 1974). Pavlov (1969) found an optomotor response in all 53 species he examined, although it was weaker in demersal species. Protasov (1968) reported that some demersal species did not have an optomotor reaction. Contact with the bottom may inhibit the response in demersal species (Harden Jones 1963). This may explain why hardhead catfish can be easily induced to exit trawls. There are differences between species in the degree and speed of the response (Arnold 1974). For example, stream-dwelling freshwater species had a faster optomotor reaction than lake dwellers (Clausen 1931).

The optomotor response is stronger in schooling species and when several fish are swimming together, and may be important in maintaining schools (Shaw and Tucker 1965). Certain species, present in large numbers, display ordered behavior by swimming between the trawl wings parallel to each other and with equal spacing between fish (Main and Sangster 1981). Schools of Pacific herring, *Clupea pallasi*, within a trawl maintained a position relative to an area of the webbing and did not pass through the meshes. However, members of herring schools outside the trawl swam through the meshes into the net on several occasions (High and Lusz 1966). In this study, the snapper also went through the meshes into the net during several of the preliminary experiments. Individuals that escaped the net often went back into the net through the escape openings, particularly when the solid panels were used.

The age of the fish can also affect the level of response. The optomotor response is stronger in juvenile fish (Pavlov 1969). The response is visual, and sufficient light (10^{-7} to 10^{-4} lux) is necessary for it to occur (Pavlov 1969). At light intensities below threshold vision, fish show no ordered pattern of behavior when confronted with a trawl because of the lack of an optomotor reaction (Glass and Wardle 1989; Walsh and Hickey 1993).

Although the optomotor response in juvenile snapper appears to be strong, agonistic behavior may override it under some circumstances. The snapper may attempt to keep station with a moving trawl, but aggressive actions of dominant individuals may prevent subordinates from doing so. Quick movements of objects or other fishes may also disrupt the optomotor response. Some schools of Pacific herring scattered in all directions through the meshes when subjected to the sudden release of scuba air bubbles (High and Lusz 1966). The juvenile snapper in the flume moved away from the decoys or the one-year-old snapper when they moved rapidly. Slow movements had little effect; the snapper would merely move out of the way, or in the case of the larger snapper, frequently draft behind them.

The avoidance reaction is the other major aspect involved in the response of fishes to trawls (Wardle 1993). A group of fish respond to a moving trawl door by skirting around it; individuals that are between the trawl doors are then herded toward the trawl by the cables (Wardle 1993). The cloud of disturbed sediment behind trawl doors and cables can reinforce their effectiveness as herding devices (Hemmings 1969; Martyshevskii and Korotkov 1968). Visual responses to trawling gear differ between day and night and with changes in turbidity (Watson et al. 1992). Orientation of Atlantic cod and haddock to the direction of tow increased at night, but herding by the trawl doors and cables decreased (Beamish 1969). However,

Hemmings (1969) pointed out that only small numbers of luminescent dinoflagellates or ctenophores would be necessary to make trawl boards and cables visible under seemingly "dark" conditions.

Nonvisual senses may also influence the response of fishes to trawls. For example, trawl doors and cables generate low-frequency sounds (Hemmings 1969). Vessel noise during trawling will cause avoidance reactions by demersal species (Ona and Godø 1988). The snapper in the flume exhibited a fright response when subjected to noises such as tapping on the sides of the flume. However, observations suggest that the senses of hearing, pressure, and touch, which are still available to fishes in the dark, are insufficient to generate the characteristic ordered daylight behavior in fishes (Wardle 1986; Walsh and Hickey 1993).

When a trawl is equipped with a BRD, red snapper maintain position behind parts of the device where water flows are slower and more turbulent. Many individuals remain in the trawl, often in sight of the opening. The snapper that leave the trawl during a tow will often follow the trawl outside the net or behind the codend (Workman and Foster 1994). Escaped snapper in the flume also swam along the outside of the net. Fishes primarily escape through BRD openings either during trawl haulback or when crowding occurs near openings. Crowding of fishes within the trawl, slowing trawl speed prior to haulback, haulback, and ambient pressure changes as a trawl is hauled up in the water column may override the optomotor response (Watson et al. 1992). Species that do not appear to have an optomotor response would exit trawls during a tow, and exclusion rates for these species approached 100% (Watson et al. 1992).

CHAPTER 3

AGONISTIC BEHAVIOR AND TERRITORIALITY OF JUVENILE RED SNAPPER

Introduction

Small juvenile red snapper are typically found near the bottom, associated with small structures, objects, or burrow openings (Workman and Foster 1994). Agonistic behavior by larger juveniles or adults may preclude juveniles from occupying sites associated with larger structures (Bailey 1995). More complex structures may be used as refuge, and simpler structures for orientation (Workman and Foster 1994). Out of 12 encounters with juvenile red snapper by divers and remotely operated vehicles off the Mississippi coast, 10 individuals were solitary, and the others were in groups of two and six snapper (Workman and Foster 1994).

Some species in the snapper family (Lutjanidae) school (Longley and Hildebrand 1941; Potts 1970; Beaumariage and Bullock 1976; Thompson and Munro 1974). Thresher (1984) suggested that snappers form loose aggregations during the daytime and spread out at night to feed. A related species, the mutton snapper, *Lutjanus analis*, establishes dominance hierarchies in patch reef systems (Mueller 1995; Mueller et al. 1994).

Agonistic behavior was observed among the juvenile red snapper during the panel experiments. Since the agonistic behavior affected fish escapement, it was hypothesized that behavior could play a critical role in how snapper relate to trawls and BRD's. For example, this intrinsic behavior could override any cues to leave the trawl. Therefore, additional experiments were designed to examine the factors affecting agonistic behavior, including: increasing fish density with and without a reef, low and high levels of constant fish density, and low water velocities. A better understanding of behavior could suggest methods by which bycatch can be reduced.

Methods

Increasing Fish Density

Several experiments were conducted to examine the effects of increasing fish density on agonistic behavior. In the bare-tank experiments, a 61-mm long section of the flume tank working channel was blocked off at each end with 2.54-cm square plastic mesh. The drive unit of the flume was not turned on during this experiment, although the flume was run for several minutes prior to each replicate to circulate the water. Individuals were randomly netted from the circular holding tanks about 10 minutes before they were to be used. These snapper were placed into a bucket, and flume tank water was gently added to acclimate the fish. Two juveniles were initially placed in the flume tank. An additional fish was added at 30-min intervals, to a total of 13 fish (6 h). All snapper were between 60 and 70 mm in length (TL). Three replicate experiments were conducted with different individuals.

The bare-tank experiment was repeated with the addition of an artificial reef (Figure 3.1). This reef was constructed of a 30.5- by 30.5-cm square section of polypropylene trawl webbing. Unraveled 30.5-cm sections of polypropylene rope were doubled and tied to the webbing at 5-cm intervals. The reef was anchored to the center of the right side of the tank by threading two 3.2-mm diameter steel rods through the front and back edges of the webbing, and inserting the rod ends through the lowest row of square plastic mesh. The reef was constructed similarly to the webbing reefs off Pascagoula, Mississippi, from which some of the snapper used in the experiments were collected. The reef occupied one-sixth of the tank bottom area. Three replicates were conducted with different individuals.

The agonistic acts of snapper in the increasing density experiments were counted for each 5-min interval. However, when the reef was present, two types of

Figure 3.1. Picture of tank setup with reef.

aggressive snapper were distinguished: resident juveniles that defended the reef (and spent much time in the narrow space under the reef) and other (nonresident) fish. The period of time a resident fish spent under the artificial reef, and the number of times a resident fish went under the reef per 30-min period, were also recorded.

To examine whether the presence of the artificial reef affected the level of agonistic behavior, data from the increasing-density experiments were analyzed with the model: log (agonistic acts + 1) = tank, time, and the interaction of these terms. Tanks were bare tank and reef tank. Each 6-h experiment was divided into three equal time periods (early, mid, and late).

Constant Fish Density

To distinguish between the effects of fish density and time, additional experiments were conducted with a fixed number of snapper throughout each experiment. Groups of five (low density) and 11 (high density) snapper were placed into the tank and observed over a six-hour period. Agonistic acts were recorded as described previously. Three replicates were done at each density level with different individuals.

To examine whether the level of agonistic behavior increased at higher fish densities, data from the constant-density experiments were analyzed with the model: log (agonistic acts + 1) = density, time, and the interaction of these terms. Densities were five fish and 11 fish. Each 6-h experiment was divided into three equal time periods (early, mid, and late).

Water Flow

Additional experiments were designed to examine the effects of water flow on agonistic activity. The flume tank was set up as described above for the experiments in the bare tank. Three snapper were placed in the flume for two hours. The first

hour was conducted with no water flow. The flume was then turned on to maintain a 10-cm/sec water flow for the second hour. Three replicate experiments were conducted with different individuals. To examine the effect of time on the number of interactions, a reciprocal experiment was conducted. Three replicates with different individuals were done with the water flow turned on during the first hour and then off during the second. Both reciprocal sets of experiments (flow then no flow and no flow then flow) were repeated with different snapper and the water flow set at 20 cm/sec.

Agonistic acts were recorded as described previously. The positions of the snapper at the end of each 5-min period were also noted to examine whether the fish altered positions in response to the water flow. For this, the tank was partitioned into an upper and lower level and each level was divided into an upcurrent and a downcurrent half. The number of snapper in each of the four sections was recorded.

Data for the water flow experiments was analyzed with the model: log (agonistic acts + 1) = type, flow, time, and the interactions of these terms. Types were flow then no flow and no flow then flow. Flows were 0, 10, and 20 cm/sec, and time periods were early (< 20 min), mid (20-40 min), and late (40-60 min).

Field Observations

In an effort to capture juvenile red snapper off the coast of Louisiana for use in this study, several webbing fish attractant reefs (with and without chafing gear) were placed approximately 31 m off an oil rig in the South Timbalier area (ST 107A) on May 21, 1995, at a depth of 26 m. On July 27, 1995, a larger reef with unraveled polyethylene rope strands tied at about 13-cm intervals was placed nearby.

Observations of juvenile red snapper were made while diving on these fish attractant reefs and on numerous other dives in waters off Louisiana, Mississippi, and

Florida. Behavior of juvenile and adult snapper was examined from videotapes recorded by NMFS divers at the Harvesting Systems Branch in Pascagoula, Mississippi.

Results

General Behavior

The types of aggressive interactions among the snapper in the experiments varied in intensity. The minimum overt act that was scored as an agonistic behavior in these experiments occurred when an aggressor swam rapidly at another individual. The most aggressive acts, observed on several occasions, were when two snapper grasped each other by the mouth and wrestled around the tank. Aggression was highest between similar-sized fish. The aggressors were frequently smaller than the fish they attacked. Resident fish in the reef experiments were not generally the largest fish.

Dominant snapper often displayed an erect dorsal fin and lowered pelvic fins; the body was typically angled with the head downwards (Figure 3.2). When an aggressor swam toward another individual, non-aggressive fish responded by swimming rapidly away. Other snapper adopted an aggressive posture, and either maintained their position or swam toward the aggressor. An aggressor typically attacked several other snapper during a particular 30-min interval. However, as the number of fish in the tank increased fish were chased into the paths of other fish, initiating further attacks. Snapper typically did not disperse within the tank, but frequently remained bunched up, even if agonistic behavior was occurring (Figure 3.3).

Figure 3.2. Juvenile red snapper on left shows typical dominance posturing.

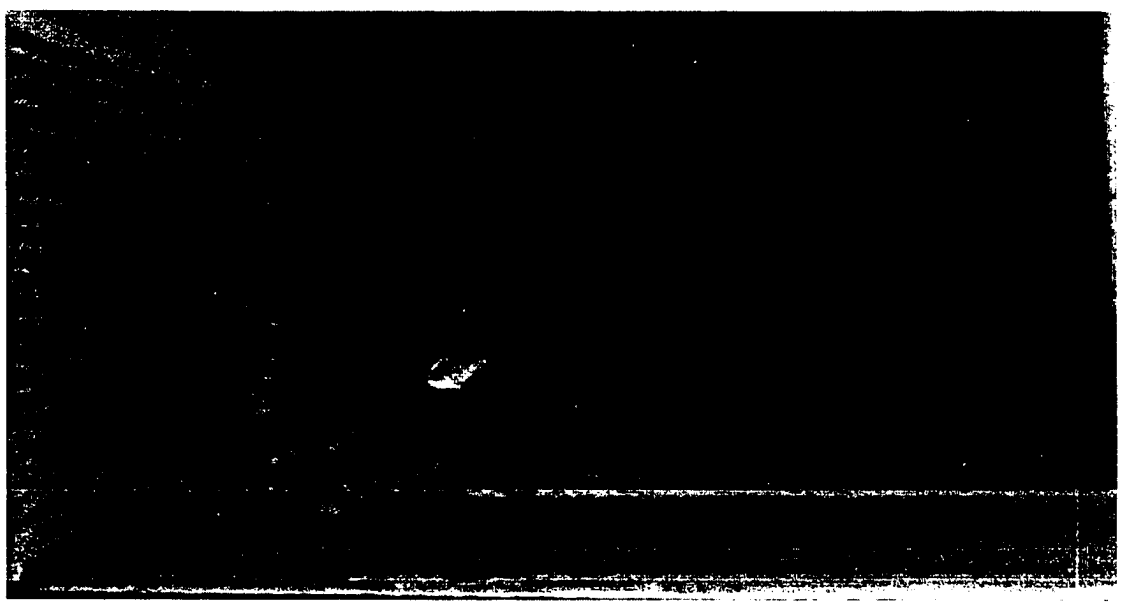


Figure 3.3. Aggregating behavior of fish in agonistic behavior experiments.

Increasing Fish Density

The snapper in the three replicates in the bare tank displayed 3799 agonistic acts over the 18-h period. There were 17.6 ± 12.8 (mean ± standard error) agonistic acts per 5-minute interval (Table 3.1). Agonistic acts for each of the replicates were distributed similarly (Figure 3.4). In each case, the level of agonistic behavior peaked at 5 h, when 11 fish were present. During a given 30-min period, these snapper tended to have the highest agonistic activity five to 10 min after the addition of a new individual (Table 3.1). For a brief (30-s to 1-min) period after a new fish was introduced, the snapper already present in the tank would flee to the tank corners and sides. Therefore, the number of agonistic acts for the initial 5-min period occurred over a slightly shorter time frame than the other five time intervals.

Snapper in the three replicates with a reef present had 7480 agonistic acts, 34.4 ± 28.1 acts per 5-minute interval (Table 3.1). This amount was double the number of agonistic acts in the bare tank experiment. In each replicate, one or two individuals (resident fish) took up station under the reef and chased away other snapper (nonresident fish) that got near, or attempted to go under the reef. The distribution of agonistic acts initiated by the snapper with the reef present was strongly dominated by five resident individuals (3610 acts) compared to the more numerous nonresident fish (3870 acts--Table 3.2). Although the nonresident snapper behaved similarly between replicates (Figure 3.5), the actions of the resident fish differed (Figure 3.6).

Five snapper aggressively defended the reef habitat from other individuals in the tank in the three experiments. In the first replicate, a 65-mm snapper (Fish 1A) took up residence under the reef 35 min into the experiment, after the third snapper was added (Figure 3.6). A 70-mm individual (Fish 1B) displaced Fish 1A about 3.5

Table 3.1. Mean number of agonistic acts, by time interval, after the introduction of additional fish (increasing-density experiments) and, per five-minute time interval (constant-density experiments), total acts per treatment, and mean number of agonistic acts per 5-minute interval.

	Increasing Density		Constant Density	
Time Interval (min)	Bare	Reef	5 fish	11 fish
0-5	190.3 ± 31.1	340.3 ± 154.0	74.7 ± 11.9	247.0 ± 36.1
5-10	233.7 ± 23.4	468.0 ± 231.6	75.3 ± 10.2	244.7 ± 36.1
10-15	216.7 ± 9.4	461.0 ± 233.8	74.7 ± 3.8	261.0 ± 58.0
15-20	214.0 ± 12.2	409.0 ± 180.8	81.0 ± 3.6	257.3 ± 40.4
20-25	218.7 ± 49.5	406.0 ± 162.2	74.7 ± 1.5	255.3 ± 68.1
25-30	193.0 ± 24.6	409.0 ± 165.1	77.3 ± 11.1	233.0 ± 49.9
Total Acts Per Treatment	3799	7480	1373	4495
Mean ± Standard Error of Acts Per 5-Minute Interval	17.6 ± 12.8	34.4 ± 28.1	6.4 ± 4.0	20.8 ± 11.0

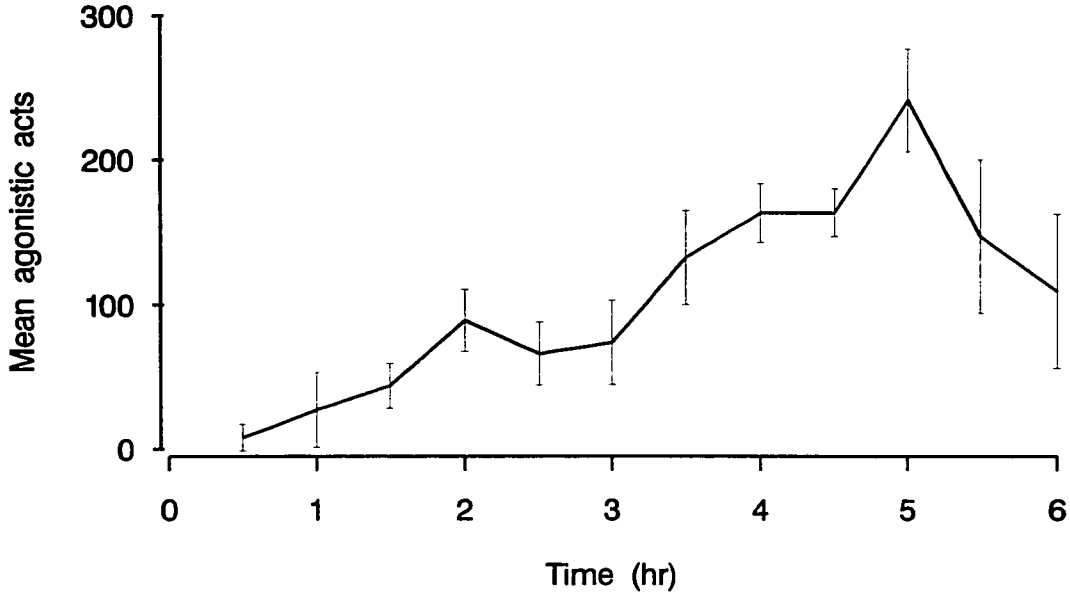


Figure 3.4. Mean and standard error of overt agonistic acts, per 30-min interval, for juvenile red snapper in increasing-density replicates in the bare tank.

Table 3.2. The number of agonistic acts, by time interval, total acts, and mean acts per 5-minute interval for the experiments with the reef present, by reef fish type.

Time interval (min)	Reef Fish Type	
	Residents	Non-residents
0-5	155.0 ± 127.0	185.3 ± 38.4
5-10	238.7 ± 181.3	229.3 ± 55.3
10-15	232.0 ± 153.4	229.0 ± 90.9
15-20	197.0 ± 133.4	212.0 ± 74.9
20-25	183.3 ± 115.6	222.7 ± 61.1
25-30	197.3 ± 88.2	211.7 ± 81.7
Total Acts Per Fish Type	3610	3870
Mean Acts Per 5-minute Interval	16.5 ± 16.4	17.9 ± 16.3

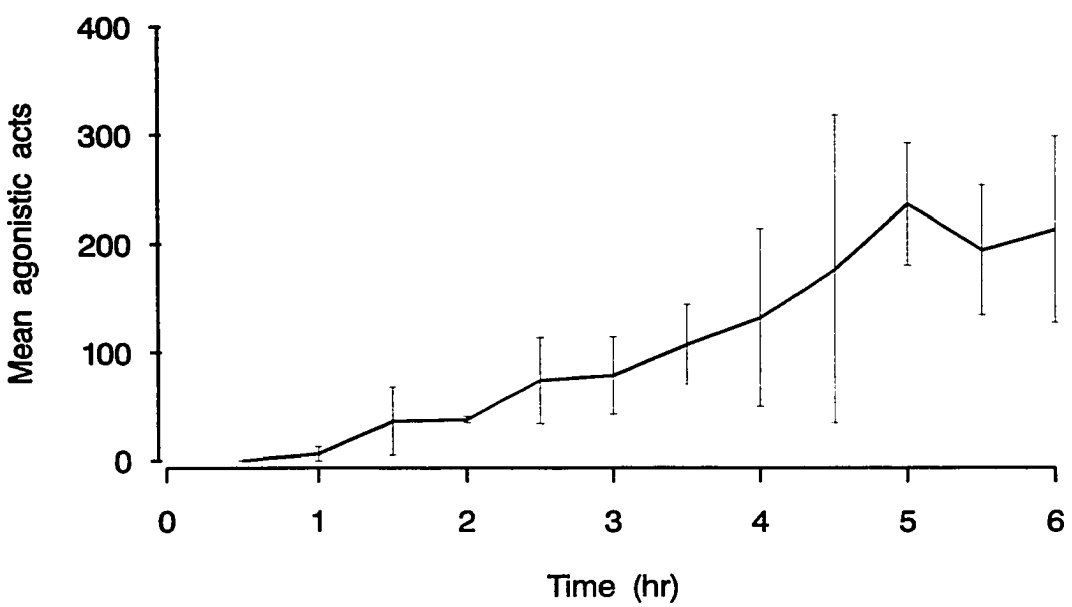


Figure 3.5. Mean and standard error of overt agonistic acts, per 30-min interval, for nonresident juvenile red snapper in increasing-density replicates with reef.

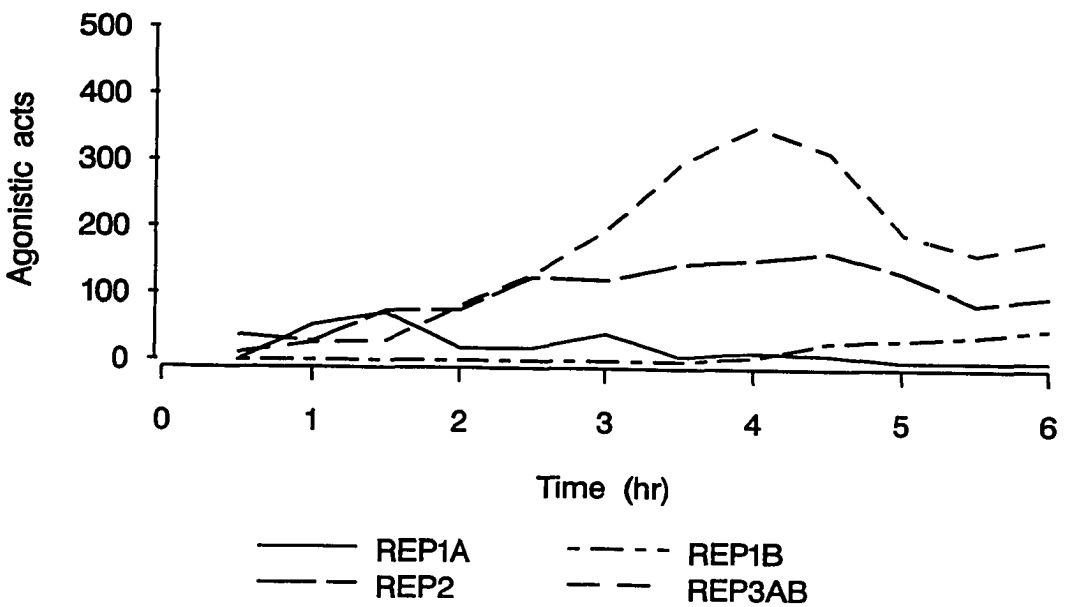


Figure 3.6. Number of overt agonistic acts, per 30-min interval, for resident juvenile red snapper in the increasing-density replicates with reef.

hours later, when nine and 10 snapper were present (Figure 3.7). Fish 1B remained associated with the reef until experiment ended. The number of agonistic acts initiated by the resident snapper were: Fish 1A, 233 and Fish 1B, 157 (Table 3.2). The remaining 842 agonistic acts were initiated by the nonresident fish, Fish 1A after it was permanently displaced from the reef, and Fish 1A and 1B before they became the resident fish (Table 3.2). Within the first 30-min period of the second replicate, a 60-mm fish (Fish 2A) went under the reef. Fish 2A remained the resident until the experiment ended and initiated 1244 agonistic acts. There were 1610 acts among the nonresident snapper (Table 3.2). In the third replicate, two individuals (Fish 3A and B) went under the reef at the same time and attacked each other for a short period. Subsequently, these snapper remained under the reef together and initiated agonistic acts against the other individuals in the tank. These two fish initiated 1976 agonistic acts, while the nonresident snapper had 1418 acts (Table 3.2).

In general, when resident snapper were away from the reef, they were typically the aggressors, and few agonistic acts occurred among the nonresident fish during these periods. When the resident snapper was under the reef, however, the nonresident individuals in the tank often alternately chased one another. Like the fish in the bare tank, during a given 30-min period, these snapper tended to have the highest agonistic activity five to 10 min after a new individual was added (Table 3.1). However, when the data for each replicate are examined (Table 3.2), the pattern often differed for the resident snapper, although it was consistent for the nonresident fish.

The percent of time the resident snapper remained under the reef is illustrated in Figure 3.7. The two resident individuals in replicate one stayed under the reef 23 and 28% of the time (Fish 1A, 1.7 h; Fish 1B, 1.4 h). Continuous intervals under the

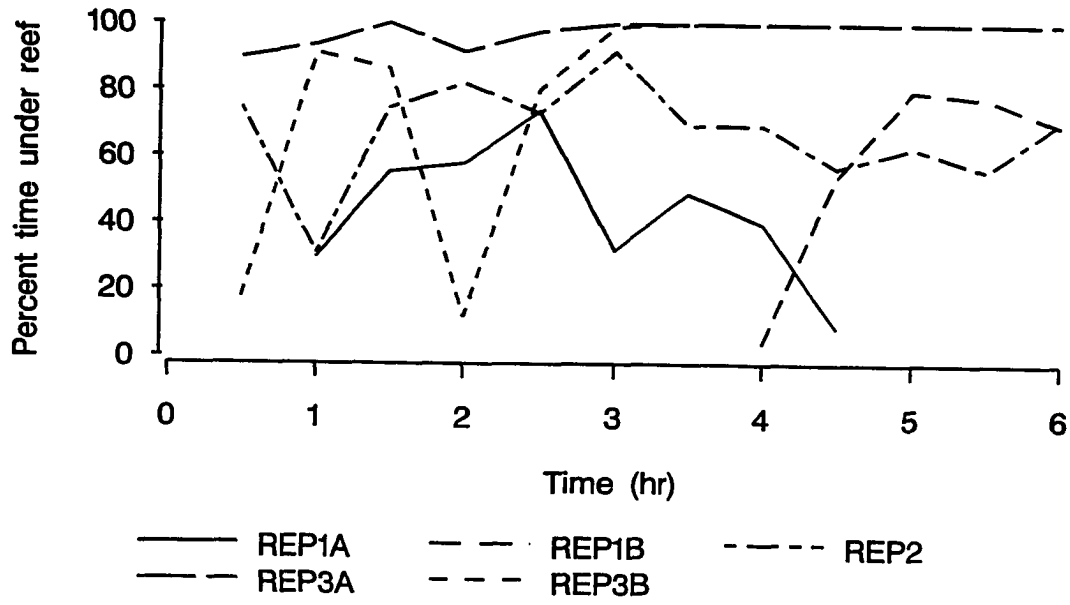


Figure 3.7. Percent time spent under reef, per 30-min interval, for resident juvenile red snapper in the increasing-density replicates with reef.

reef ranged from 3 s to 15.3 min, with a mean time of about 1.6 min. Fish 2A stayed under the reef 68% of the time (mean, 1.3 min; minimum, 1 s; maximum, 7.6 min). Fish 3A in the third replicate spent 97% of the time under the reef, while Fish 3B was under the reef 82% of the time. Continuous intervals under the reef for these snapper ranged from 1 s to 30 min (means: 17.6 min, 3A; 10.1 min, 3B).

Comparison of bare and reef tanks

Overall, the mean number of agonistic acts was significantly higher in the reef tank (21.4) than the bare tank (11.9 - $P>F<0.01$ - Table 3.3). The mean number of agonistic acts also differed among the three time intervals (early, 5.2; mid, 21.8; late, 34.9 - $P>F=0.001$).

Constant Fish Density

At low-constant densities (5 snapper), the number of agonistic acts was fairly uniform for all replicates (Figure 3.8), although the number of acts for replicate 3 peaked at the one-hour interval. The three replicates had a total of 1373 agonistic acts, a mean of 1.3 acts per minute (Table 3.1).

At high-constant densities (11 snapper), the most acts occurred during the first hour (Figure 3.9), although replicate 3 had a secondary peak at 3 to 3.5 h. At high-constant densities, a total of 4495 agonistic acts occurred during the three replicates, a mean of 4.2 acts per minute (Table 3.1). There was little difference in agonistic activity among the time intervals for fish in either constant-density experiment.

There was a significant treatment-by-time interaction for the constant-density data ($P>F<0.01$ - Table 3.4). Although the mean number of agonistic acts was always higher at high densities than at low densities, the difference between the two densities was greatest during the first two hours of the experiment (Figure 3.10).

Table 3.3. Results of analysis of variance for log (agonistic acts + 1) for the increasing-density experiments. Tanks were: bare tank and reef tank. Times were: early (1-2 h), mid (3-4 h), and late (5-6 h).

Source	DF	Mean Square	F-value	Pr > F
Tank	1	33.06	55.70	<0.01
Time	2	120.65	203.30	<0.01
Tank*Time	2	0.66	1.11	0.33
Error	426	0.59		
Corrected Total	431			

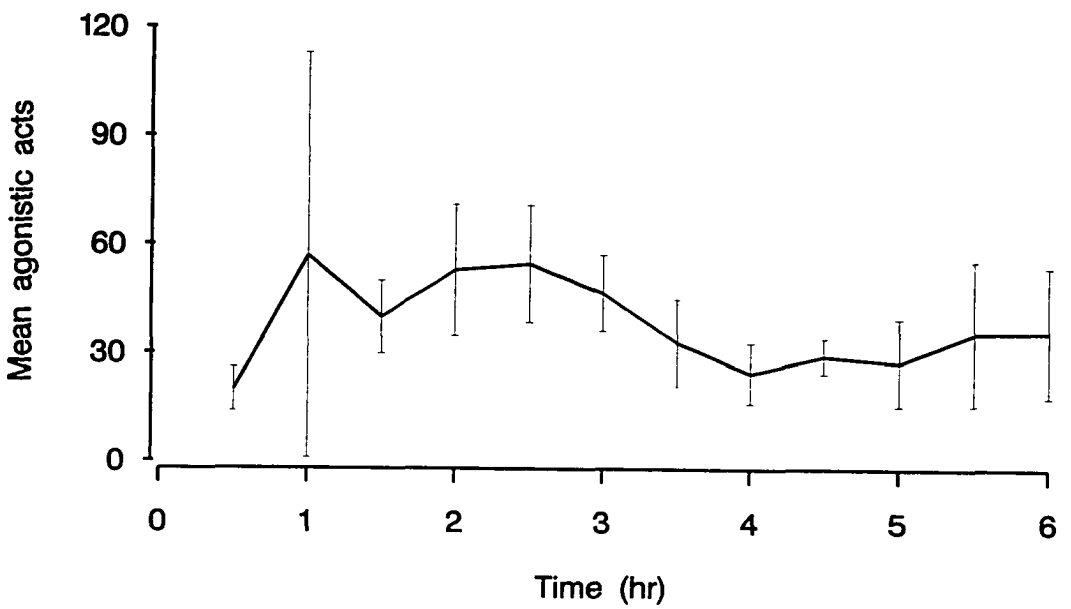


Figure 3.8. Mean and standard error of overt agonistic acts, per 30-min interval, for juvenile red snapper in 5-fish (low) constant-density replicates.

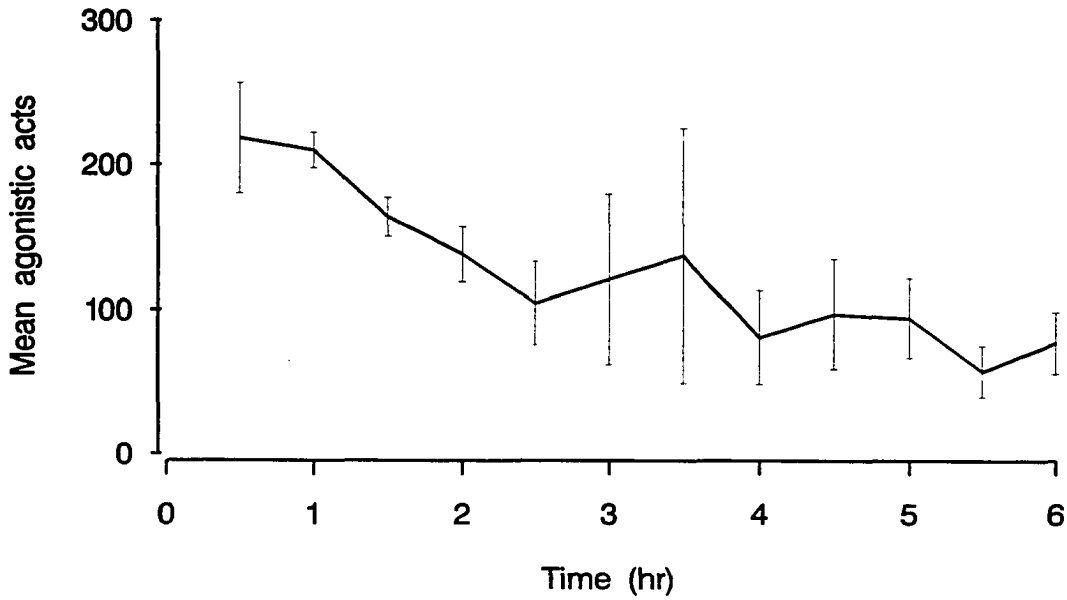


Figure 3.9. Mean and standard error of overt agonistic acts, per 30-min interval, for juvenile red snapper in 11-fish (high) constant density replicates.

Table 3.4. Results of analysis of variance on log (agonistic acts + 1) for the constant-density experiments. Treatments were: 5 fish and 11 fish. Times were: early (1-2 h), mid (3-4 h), and late (5-6 h).

Source	DF	Mean Square	F-value	Pr>F
Treatment	1	129.26	658.22	<0.01
Time	2	7.34	37.38	<0.01
Treatment*Time	2	4.58	23.33	<0.01
Error	426	0.20		
Corrected Total	431			

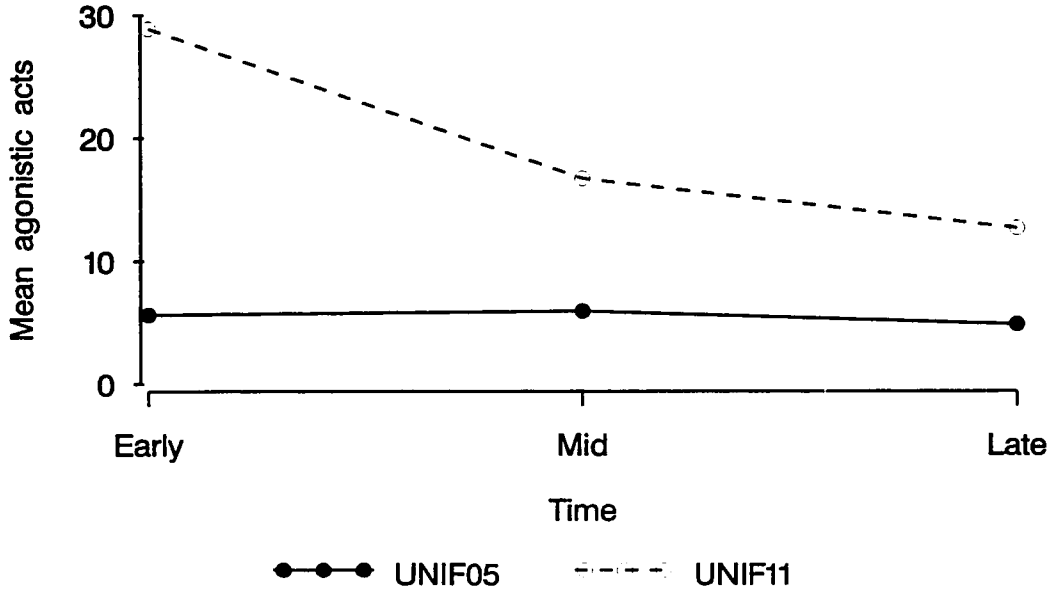


Figure 3.10. Mean number of overt agonistic acts, per 2-h interval, for juvenile red snapper, by density (UNIF05 = low density, UNIF11 = high density), in constant-density experiments.

Comparison of increasing and constant fish density

When the replicates for each treatment type were averaged, several trends were apparent (Figure 3.11). During the first two hours of the experiments, snapper in the high-constant-density experiments had the most agonistic acts, however, the level of agonistic behavior in this experiment subsequently declined. The levels of agonistic aggression in the low-constant and increasing-density experiments were more similar early in the experiments. However, the number of acts in the low-constant-density experiment remained low for the duration of the experiment. After the first two hours, as more individuals were added to the bare and reef tanks, the number of acts increased until the density reached 11 snapper per 0.16 m^3 of water, then declined. Interestingly, the mean number of acts for the bare tank with 11 individuals at 5 h peaked at nearly the same level as the snapper in the constant-high density (11 snapper) experiment at 30 min. Although the number of agonistic acts in the bare and reef tanks peaked at the same time, agonistic activity in the reef tank was nearly twice as high.

Water Flow

Agonistic activity under flow conditions in the no flow then 10 cm/sec flow (1 hour no flow/1 hour of flow) replicates (Figure 3.12) was 2.3 times higher than those with no flow (Table 3.5). Similarly, replicates under reciprocal conditions (10-cm/sec flow then no flow--Figure 3.13), had 2.2 times more agonistic acts under flow than no flow. The replicates under no flow then 20 cm/sec flow (Figure 3.14) had agonistic activity levels 2.4 times higher under flow conditions than with no flow (Table 3.5). The reciprocal replicates (20-cm/sec flow then no flow--Figure 3.15), had three times more agonistic acts under flow than no flow.

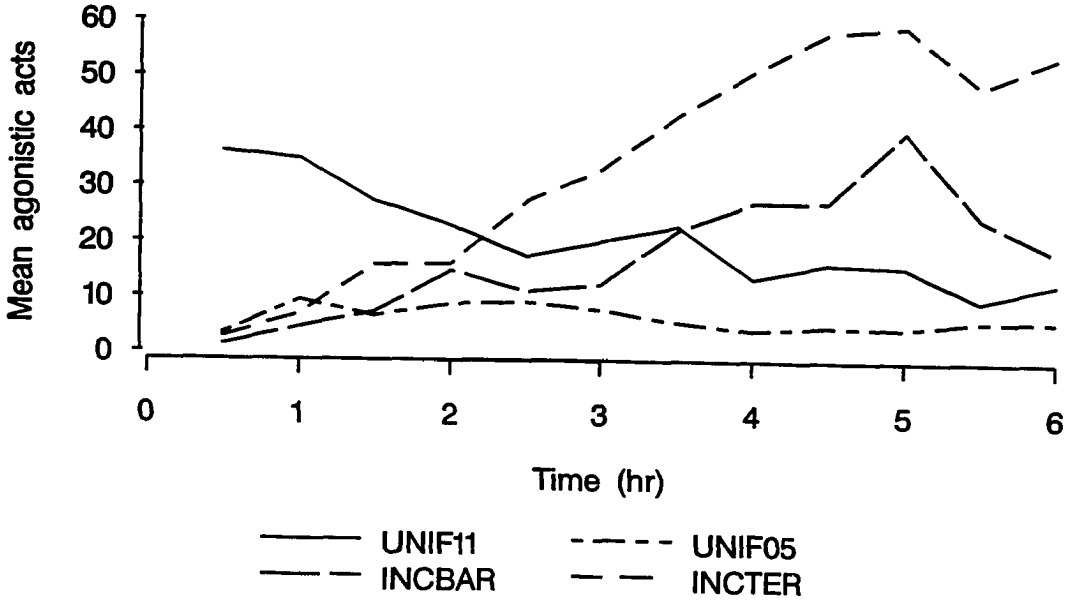


Figure 3.11. Mean number of overt agonistic acts, per 30-min interval, for juvenile red snapper, by treatment (UNIF05 = low constant density, UNIF11 = high constant density, INCBAR = increasing density bare tank, INCTER = increasing density reef tank), in agonistic behavior experiments.

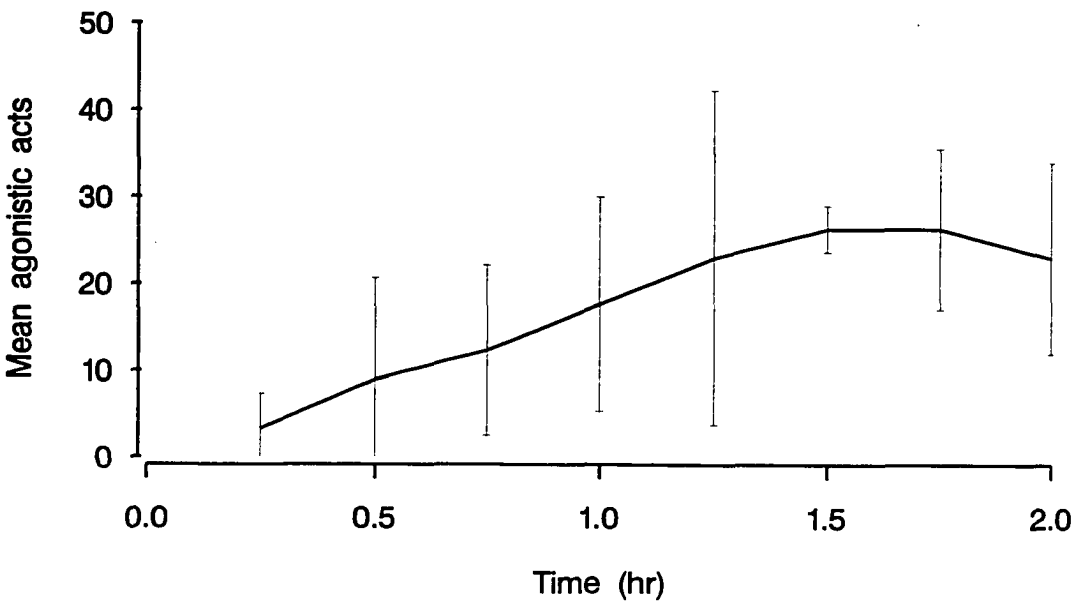


Figure 3.12. Mean and standard error of overt agonistic acts, per 15-min interval, among three juvenile red snapper in replicates under no flow then 10-cm/sec flow. Point of flow increase was at time of 1.0 hr.

Table 3.5. Mean agonistic acts and total number of acts by type and flow for the water flow experiments.

Type	Flow then no flow		No flow then flow	
Flow	Flow	No flow	No flow	Flow
		10 cm/s flow		
Mean Acts Per 5-minute Interval	9.4 ± 3.9	4.3 ± 2.1	3.5 ± 3.3	8.2 ± 4.0
Total Acts Per Type and Flow	338	154	127	296
		20 cm/s flow		
Mean Acts Per 5-minute Interval	14.8 ± 5.0	4.9 ± 2.2	5.9 ± 4.0	14.1 ± 6.4
Total Acts Per Type and Flow	534	178	211	508

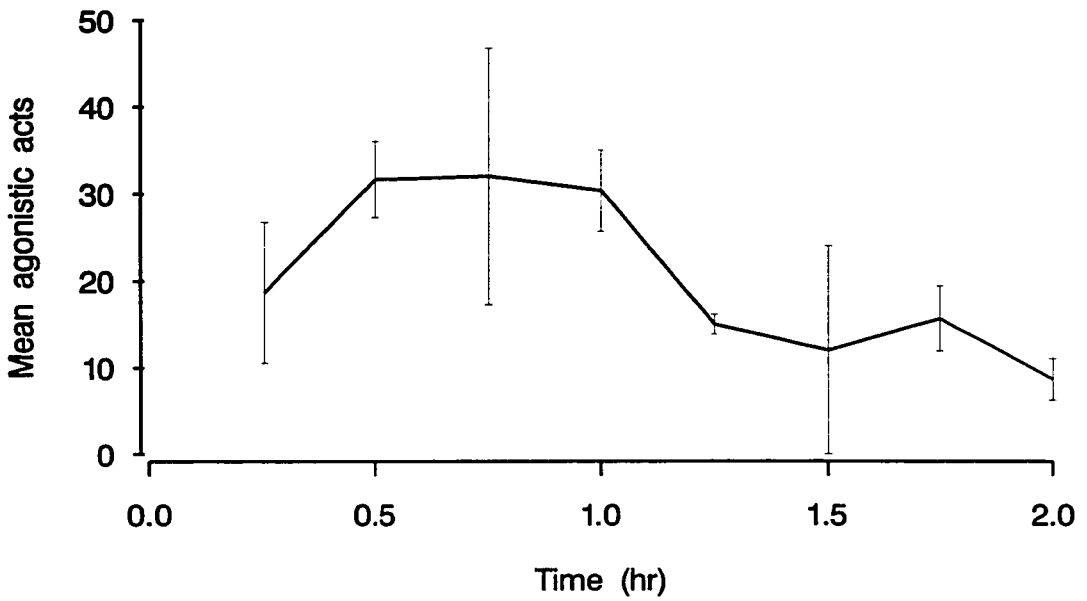


Figure 3.13. Mean and standard error of overt agonistic acts, per 15-min interval, among three juvenile red snapper in replicates under 10-cm/sec flow then no flow. Point of flow decrease was at time of 1.0 hr.

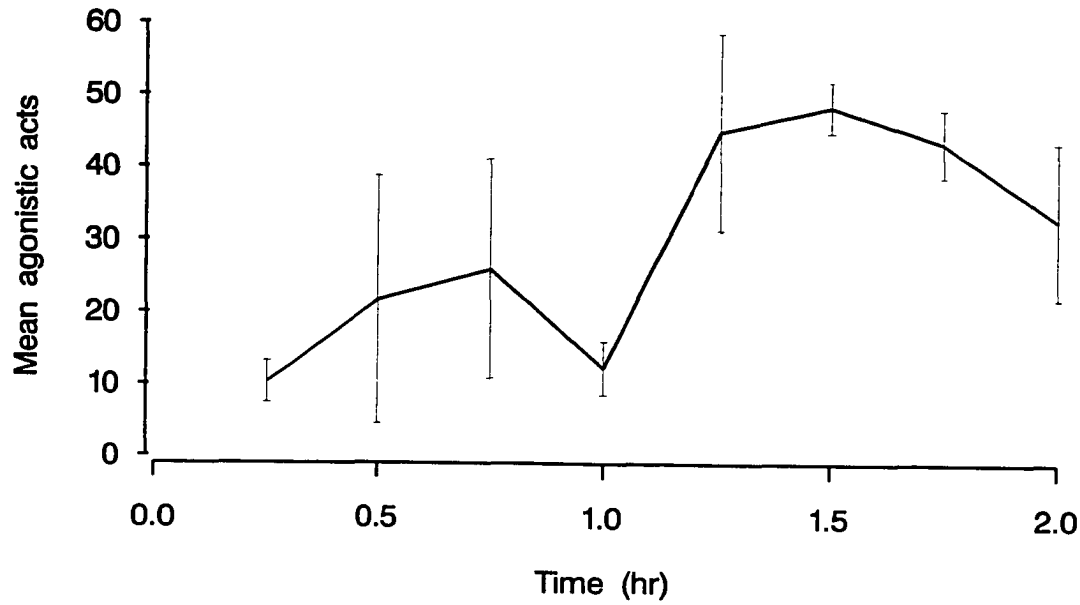


Figure 3.14. Mean and standard error of overt agonistic acts, per 15-min interval, among three juvenile red snapper in replicates under no flow then 20-cm/sec flow. Point of flow increase was at time of 1.0 hr.

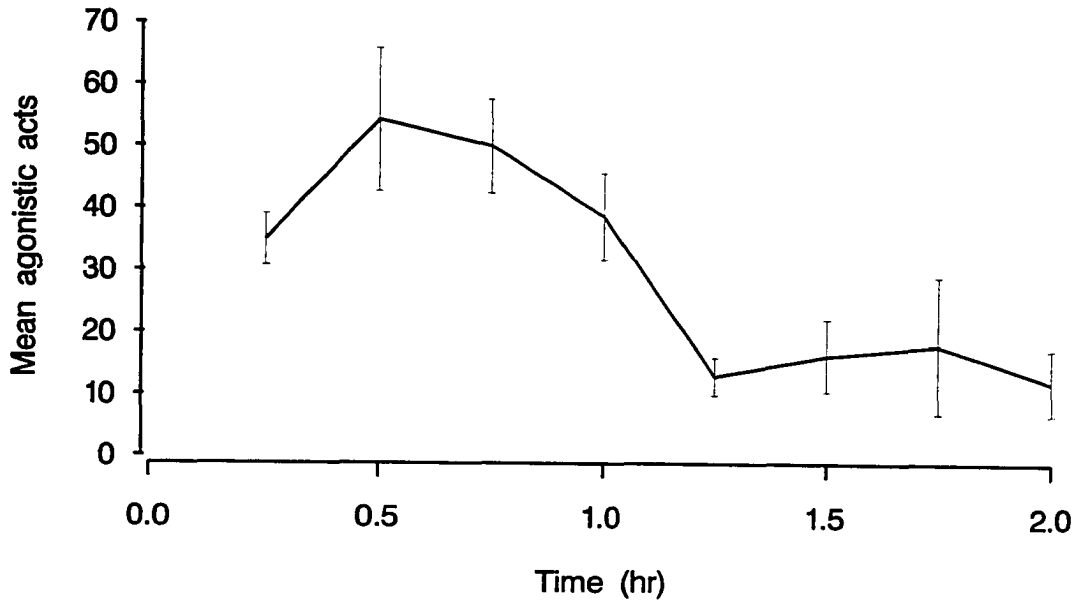


Figure 3.15. Mean and standard error of overt agonistic acts, per 15-min interval, among three juvenile red snapper in the replicates under 20-cm/sec flow then no flow. Point of flow decrease was at time of 1.0 hr.

The snapper tended to stay in the lower part of the water column under both flow conditions and ventured higher only when the current was turned off. There were no obvious trends in horizontal fish position under flow and no flow conditions. The agonistic behavior of a few snapper would frequently keep other individuals from certain locations. Although the snapper tended to be more upcurrent under no flow conditions than the 10 cm/sec flow during the no flow then flow replicates, there were no apparent differences in most of the replicates under flow then no flow (Figure 3.16). For the 20-cm/sec replicates, there were no apparent trends under either experimental condition (Figure 3.17). Individuals seemed just as likely to remain upcurrent as downcurrent when the water was turned on. Agonistic activity during the 20-cm/sec replicates was also higher.

There was a significant interaction between type, flow, and time ($P>F=0.001$ - Table 3.6). The number of agonistic acts were was always highest under the 20-cm/sec flow, followed by the 10-cm/sec flow, then the no flow conditions (Figures 3.18 and 3.19). In contrast, during the flow then no flow experiments, the mean number of agonistic acts under the three water-flow conditions was closer early in the experiments (Figure 3.18) than under the no flow then flow experiments (Figure 3.19).

Field Observations

While diving on the webbing fish attractant reefs on July 8, 1995, we observed two young-of-the-year red snapper under one reef and a school of eight juveniles on a nearby rubble pile. A school of adult snapper was also observed swimming near the rubble. No juvenile or adult snapper on or near the reefs were observed on the second trip. No fish of any species were found below about 18 m. The rig was later

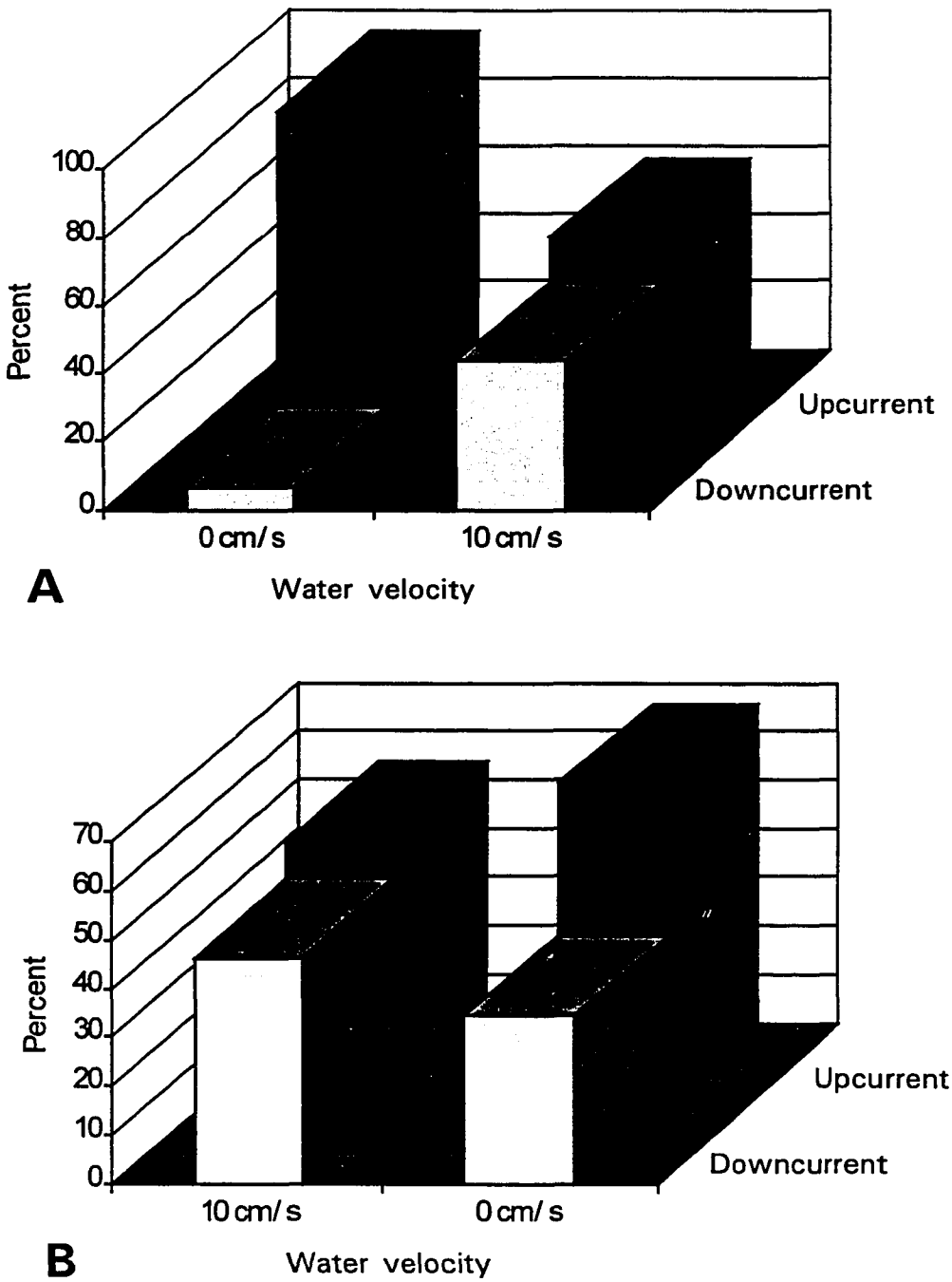
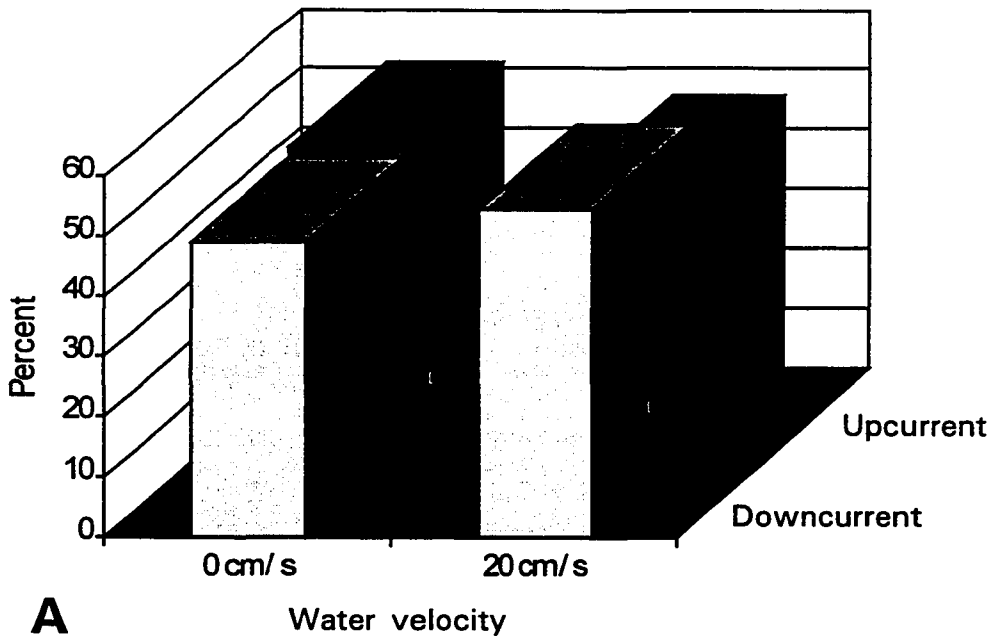


Figure 3.16. Mean percentage of snapper upcurrent and downcurrent for experiments (A) under no flow then 10-cm/sec flow and (B) 10-cm/sec flow then no flow.



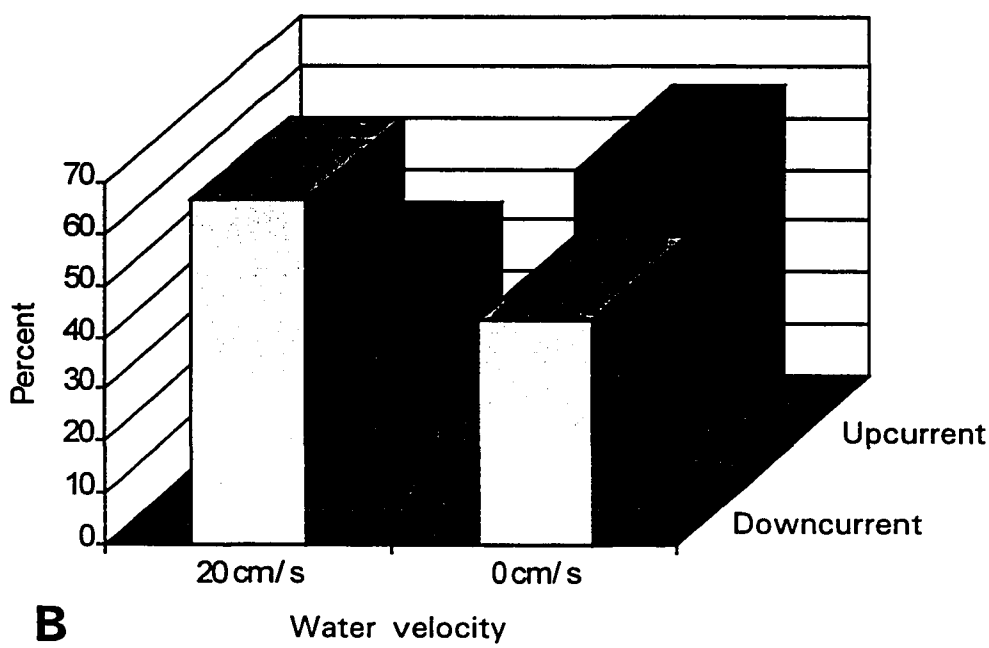


Figure 3.17. Mean percentage of snapper upcurrent and downcurrent for experiments (A) under no flow then 20-cm/sec flow and (B) 20-cm/sec flow then no flow.

Table 3.6. Results of analysis of variance for log (agonistic acts + 1) for the water flow experiments. Types were: flow then no flow and no flow then flow. Flows were 0, 10, and 20 cm/sec. Times were: early (< 20 min), mid (20-40 min), and late (40-60 min).

Source	DF	Mean Square	F-value	Pr > F
Type	1	1.01	3.56	0.06
Flow	2	31.25	110.58	<0.01
Type*Flow	2	0.01	0.04	0.96
Time	2	2.38	8.42	<0.01
Type*Time	2	0.02	0.07	0.93
Flow*Time	4	0.47	1.66	0.16
Type*Flow*Time	4	1.37	4.84	<0.01
Error	270	0.28		
Corrected Total	287			

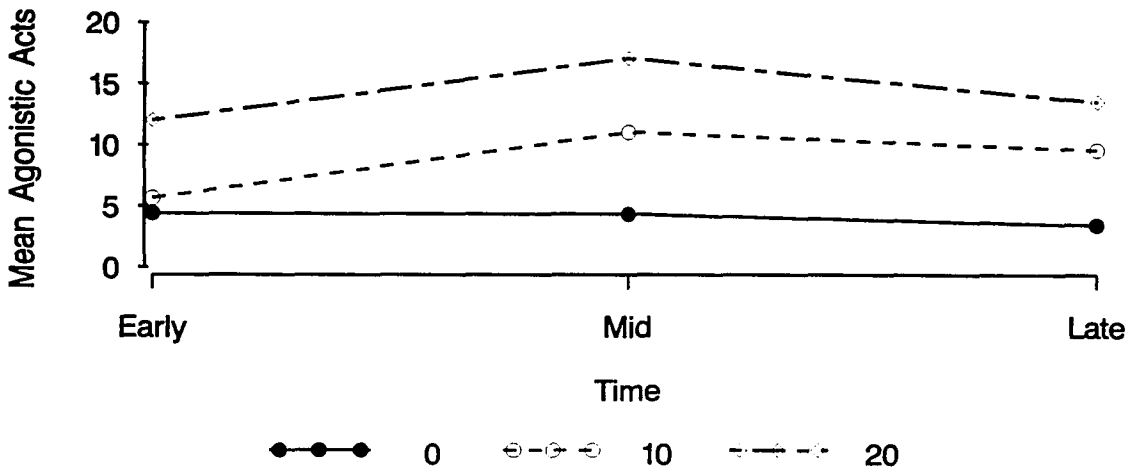


Figure 3.18. Mean agonistic acts, by time and water velocity, for the flow then no flow experiments.

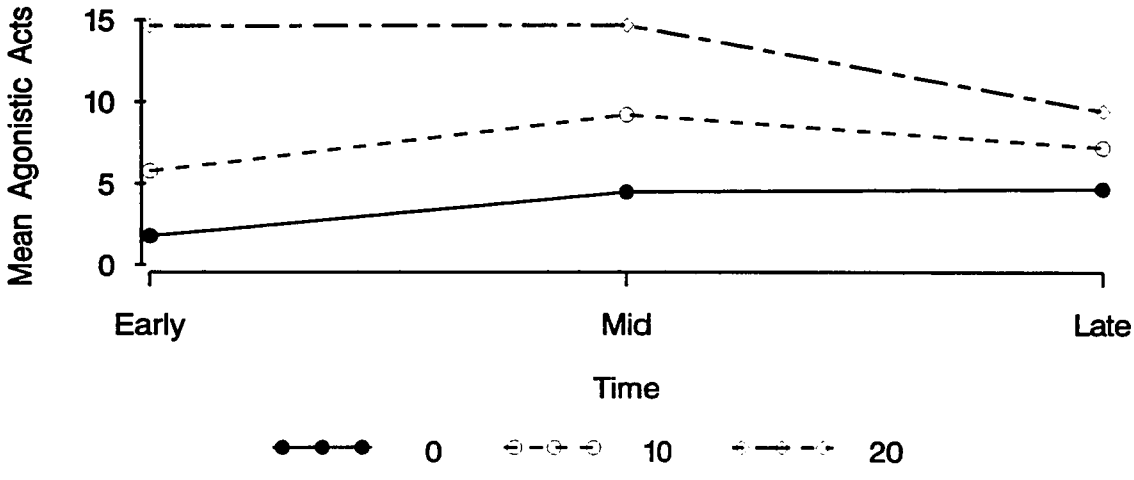


Figure 3.19. Mean agonistic acts, by time and water velocity, for the experiments under no flow then flow.

found to be inside the hypoxic zone (N. Rabalais, LUMCON, personal communication). Trips to the reefs were delayed until the hypoxic zone had dissipated.

Another dive trip was made out to the reefs on September 9, 1995. We found the two smaller reefs but could not locate the large reef with chafing gear. A large mound of trawl webbing was found approximately where the large reef had been located. Two small snapper were observed near each small reef, a school of about 10 small snapper were near the webbing mound, and a few snapper were on the fringes of rubble pile. The rubble pile had several large snapper and grouper, and the small snapper may remain near the edge to avoid predation. Subsequent dive trips to the site indicated that although juvenile snapper were using the reefs, due to the small size of the reefs, their numbers were insufficient for use in the experiments.

Discussion

Territories, Dominance Hierarchies, and Schooling

The juvenile red snapper seemed to form a dominance hierarchy or pecking order in the bare-tank experiments. However, some of these individuals remained near the ends of the blocked off section of the tank. On numerous occasions, agonistic acts appeared to be initiated by snapper attempting to keep the other fish a certain distance from the plastic mesh, particularly at the corners where the mesh touched the sides of the flume. Another possible cause of the behavior was that the square plastic mesh used to block off each end of the tank could have created, in effect, a vertical reef that elicited territorial behavior. When the flume was turned on, this territorial behavior became more apparent as individuals defended the more desirable low-flow areas.

Morse (1980) suggested that territories and social dominance hierarchies are at the opposite ends of a spectrum, along which there are many situations combining

aspects of both. Although territorial behavior may also be considered a form of dominance, dominance lacks a clear reference point in space (Morse 1980). Territorial defense may shift to a dominance hierarchy when resources become limited, then back to territories when conditions improve (Hinde 1952). For example, if favored habitat types are patchy, territorial groupings will resemble hierarchical groups (Morse 1980). When food is predictable and thinly spread, it may be feasible to defend a territory with all resources. But when food is highly clumped or unpredictable, defense may not be possible and there is a tendency to feed in aggregations (Morse 1980). Hierarchical relationships within a group may make feeding more efficient by reducing hostility, and may reduce susceptibility to predation (Morse 1980).

The density of fish in an area can also affect whether a species maintains territoriality or a dominance hierarchy. Two species of juvenile damselfish, *Pomacentrus wardii* and *P. flavicauda*, shifted from territorial behavior to dominance hierarchies when crowded (Doherty 1982). Territories and dominance hierarchies may coexist in certain situations. Young-of-the-year brook trout had a territorial structure superimposed by a dominance hierarchy. Two or three fish were dominant over three or four territorial fish, which in turn were dominant over non-territorial fish (McNichol et al. 1985). During daylight hours, the nonaggressive brook trout spent more time away from their stations feeding than did aggressive fish. The costs of defending a territory are high, not only in terms of time and energy required to defend an area and a possible increased risk of predation (Morse 1980), but also in terms of lost feeding time (McNichol et al. 1985). The major benefits of territories include increased food supply and improved protection (Morse 1980).

The resident red snapper in the reef tank were generally the dominant individuals in the tank, except for the interval in replicate one when Fish 1B displaced Fish 1A from the reef. Morse (1980) noted that owners usually prevail in territorial encounters. The resident snappers spent much time under the reef. In other situations, defending individuals may spend more time in areas where they will most likely encounter invading individuals (Morse 1980).

Snapper can develop a co-territory and defend it together, for example in reef tank replicate three. This may be similar to the *Dear Enemy* phenomenon, where adjacent territory holders reduce hostility and reduce energetic expenditures. The two snapper initially fought, but after unsuccessfully attempting to dislodge one another from the reef, aggression between these individuals ceased, and they redirected their energy towards other invading snapper. The *Dear Enemy* phenomenon is reportedly rare in fishes, although it has been observed for the wrasse, *Thalassoma duperreyi*, another reef fish (Miller 1978).

Most, although not all, fish schools lack a hierarchical structure (Morse 1980). Juvenile chum salmon are typically considered to be a schooling fish, but some individuals abandon schooling and display aggressive behavior in the presence of an easily defendable food source (Ryer and Olla 1991). Dominant juvenile chum salmon tended to swim in a tank alone, whereas the subordinates continued schooling (Ryer and Olla 1991). Fernald and Hirata (1977) noted that non-territorial *Haplochromis burtoni*, a cichlid, typically stayed in two or three relatively stationary schools of 30 to 50 fish on the edge of the colony. They observed little agonistic activity within the groups, except for occasional confrontations between non-territorial males. If conditions permit, the Manini, *Acanthurus triostegus,* tends to spread out and feed alone (Barlow 1974). However, when competition for food resources is high and

there is aggression from dominant competitors, they form tight schools and feed almost in contact with one another. Jones (1983) suggested that aggregations of one species of juvenile temperate wrasse are not schools but loose foraging groups which may be associated with preferred foraging areas. Brown and Orians (1970) considered behavior patterns such as aggregation and territoriality to be part of a continuum of space-related behavior. Juvenile snapper can apparently switch between territoriality, dominance hierarchies, and schooling in response to different situations.

Agonistic Behavior and Fish Density

The number of juvenile red snapper present in the tank affected the level of aggression among the snapper. The number of agonistic acts among the red snapper in most of the increasing-density replicates peaked at a density of 11 juveniles per 0.16 m^3 of water, then decreased as more individuals were added. Dominance relationships often lower the intensity and frequency of overt hostility (Morse 1980). For juvenile domino damselfish, *Dascyllus albisella*, the total number of chases within a group, and the number of chases per fish, were significantly related to group size (Booth 1995). Sale (1972) noted that in many species of fish, the level of agonistic activity is influenced by the degree of crowding experienced when they are put into tanks. However, this relationship is not simple. Even groups that are more crowded while sheltering in a colony of coral will show heightened agonistic behavior (Sale 1972). Other studies have shown a decrease in the number of agonistic acts at higher densities. In the juvenile temperate wrasse, *Pseudolabrus celidotus*, the rate of agonistic encounters had a bell-shaped or parabolic relationship to density (Jones 1983). The frequency of aggressive encounters increased with density when numbers were low, but when populations were crowded, most wrasses behaved

nonaggressively and foraged much of the time. Jones (1983) suggested that at high densities, the energetic cost of aggression is probably exceeded by the energy gains associated with increased foraging time. In contrast, Ferguson et al. (1983) found no effect of varying fish density on behavior of lake charr.

The number of agonistic acts in the high-constant density replicates was initially high, then dropped off, opposite to that observed in the increasing-density experiments. The snapper probably established a dominance hierarchy early in the experiment. Once the hierarchy was established, little effort was needed to maintain it, and the number of acts decreased. In the experiments where an additional individual was added at half-hour intervals, the hierarchy would have to be reestablished each time a new individual was added. Few agonistic acts occurred among the snapper under low-constant-density conditions, possibly because the chances of one individual encountering another were reduced. However, the juvenile snapper in these experiments often attempted to remain close to one another, even if agonistic behavior was involved. The snapper did not typically spread out over the available tank space, but would group in one or two areas.

At the lowest densities in these experiments, a particular juvenile red snapper would typically dominate the other individuals. However, at higher densities, snapper would alternately chase one another, and frequently, one individual would chase a second fish into the path of a third snapper that would then chase the second fish. Similarly, Morse (1980) suggested that an increase in group size allows a greater opportunity for nonlinear relationships in dominance hierarchies.

Agonistic Behavior and Fish Size

Agonism among the juvenile red snapper in this study did not appear to be related to the size of the fish as has been shown in other studies. Smaller juveniles

were just as likely to initiate aggression against slightly larger juveniles. However, all the red snapper were within a 30-mm size range (45 to 75 mm TL). When diving, however, we frequently observed larger juveniles chasing smaller red snapper. Another study indicated that sub-adult red snapper kept young-of-the-year snapper from more complex reefs (Bailey 1995). Sub-adult and adult red snapper near an oil platform appeared to partition the habitat by selecting different vertical depth locations (Render 1995). Smaller mutton snapper behaved submissively to larger fish in one study (Mueller et al. 1994). About 98% of the recorded chases by juvenile domino damselfish were directed at smaller individuals (Booth 1995). Similarly, studies of other species, including juvenile damselfish (Itzkowitz 1977) and bay goby (Grossman 1980) have found the larger fish were dominant.

The snapper appeared to have the most aggressive activity between snapper that were closest in size. Parker (1974) suggested that escalated contests should increase in frequency as the size difference between opponents decreases. Encounters among mutton snapper were more aggressive when individuals were of similar sizes (Mueller et al. 1994) and the mean number of nips was greatest between equal-sized juvenile Atlantic salmon (Symons 1968). Dill (1978) reported that large intruding juvenile coho salmon, *Oncorhynchus kisutch,* elicited approaches and displays from the defending fish at greater distances than small intruders. The tank in this study had a small area and the snapper were fairly close in size.

Although the red snapper were of similar ages, age can influence the number and intensity of agonistic acts. The intensity of agonistic behavior in juvenile chum salmon, *Oncorhynchus keta*, increased with age (Ryer and Olla 1991). Social agonistic acts did not occur in late larval-early juvenile stages of common carp, *Cyprinus carpio,* and the fish were spaced fairly uniformly throughout the entire water

volume (Panyushkin 1989). When the carp were two or three months old, however, they began schooling and did not appear to have dominance relationships (Panyushkin 1989). MacCrimmon and Robbins (1981) found a similar reduction in aggressive behavior among older juvenile smallmouth bass, compared to younger juveniles, in the presence of protective cover.

The presence of larger snapper or predators may decrease agonistic activity in small red snapper in some situations. As described in the panel experiments, placing a sub-adult snapper into the flume tank decreased the number of agonistic acts and the inter-fish distances among the juvenile snapper. Juvenile coho salmon exposed to predator-conditioned water displayed 44.9% fewer aggressive acts, and the average duration and intensity of agonistic behaviors decreased (Martel and Dill 1993).

Agonistic Behavior and Resources

Agonistic activity among the snapper may have increased with time as their hunger increased since the snapper were not fed during the experimental trials. Although food was not present, they may have displayed agonistic behavior in their search for food. Symons (1968) suggested that movements of individuals searching for food may put them in more frequent proximity to other fish and increase aggression. Although the snapper in the flume tank experiments were well-fed prior to the experiments, they would often take up pieces of debris into their mouths, then spit them out. Dill (1978) reported the least well-fed juvenile coho salmon had the highest charge velocities. Agonistic behavior by chum salmon increased in the presence of food; dominant individuals consumed 74% of the food and occupied nearly eight times more area than subordinates (Ryer and Olla 1991). Without food, the salmon tended to school, although agonism still occurred in several groups (Ryer

and Olla 1991). Agonistic behavior was significantly higher in the bay goby when food was present (Grossman 1980). In contrast, juvenile Atlantic salmon had the highest number of aggressive acts during periods of food deprivation, perhaps as an expression of an attempt to increase territorial size and dispersal (Symons 1968).

Growth rates of dominant individuals often tend to be higher than those of subordinates. Increasing social status while simultaneously decreasing group size resulted in increased growth in juvenile domino damselfish (Booth 1995). These increased growth rates may be because of differences in the quality of food items and not necessarily quantity. Small mutton snapper fed proportionally more often than medium or large individuals (Mueller et al. 1994). Small humbug damselfish, *Dascyllus aruanus*, actually fed at higher rates than larger fish, but the composition of the diet was influenced by social rank; higher-ranked fish consumed larger prey and higher percentages of copepods and animal prey (Forrester 1991). Even though adequate food is available to subordinates, they may still have lower growth rates because they either consume less food or factors such as stress may increase metabolism. Although juvenile steelhead trout, *Oncorhynchus mykiss*, were fed equal amounts, growth rates of dominant pair members were greater, on average, than those of the subordinates (Abbott and Dill 1989).

Increasing the size of the tank used in the experiments may reduce the agonistic behavior in red snapper. However, this may not always be the case, particularly since the snapper tended to aggregate. No significant difference was observed in the number of chases and nips by juvenile chum salmon in two tanks, one of which had a volume six times larger (Ryer and Olla 1991).

Some studies have indicated that the presence of reef habitat will decrease the number of agonistic acts. The frequency of agonistic behaviors by a group of

Dascyllus aruanus was influenced by the amount of shelter provided (Sale 1972). In this study, however, the presence of the reef actually increased the number of acts. The reef, combined with the actions of the territorial resident snapper, actually reduced the amount of tank area available to the nonresident fish by about half. Theoretically, this might have increased the number of agonistic acts among nonresidents since these snapper were forced into closer proximity.

Agonistic Behavior in Natural Settings

Juvenile red snapper are typically observed either singly or in small groups (Workman and Foster 1994, this study) and agonistic behavior to enforce territoriality most likely exists. Although snapper probably settle somewhat randomly, survival to the juvenile stage is low. Small artificial reefs (such as the rubble or webbing reefs where the snapper for this study were collected) can provide habitat for these small individuals. Although agonistic behavior among juvenile red snapper was observed on these reefs during this study and on other occasions by divers, the occurrence was much lower in nature than was observed in the laboratory. Again, one possibility is that the presence of divers may interfere with the natural behavior of snapper. More likely though is that territorial disputes between the fish present on the reef could have already occurred prior to diver visits. Little reinforcement may be necessary to maintain established territories or dominance hierarchies. The larger size of the reefs, more available habitat, and the unconfining surroundings could reduce agonistic behavior in the wild.

CHAPTER 4

SUMMARY AND CONCLUSIONS
HABITS AND HABITATS OF RED SNAPPER AND BYCATCH REDUCTION

Life History Strategies and Behavior of Red Snapper

Analysis of mitochondrial DNA (mtDNA) indicated that red snapper in the northern Gulf of Mexico are a single population (Camper et al. 1993; Gold et al. 1997). However, this technique may not be able to discern between recently-derived populations if significant differences in mtDNA haplotype frequencies have not had sufficient time to accumulate (Gold et al. 1997).

In the western Gulf of Mexico, red snapper typically spawn from June through September, with a peak in July and August. They may spawn as early as April (Bradley and Bryan 1975) or May (Goodyear 1992; Render 1995). A second spawning peak off the coast of Texas during the fall was suggested by Bradley and Bryan (1975). Although Arnold et al. (1978) observed spawning in captive red snapper, it has rarely been observed in nature. Moe (1963) reported that spawning occurred at 18 and 37 m depths off northwest Florida. Snapper may also spawn off Texas within waters 37 m in depth, although Bradley and Bryan (1975) did not observe spawning snapper. Environmental cues such as temperature, photoperiod, and lunar cycle may influence timing of reproduction in many snapper species (Grimes 1987).

Red snapper eggs are pelagic, and hatched in the laboratory 20 h after fertilization at 27 °C (Minton et al. 1983) and 24 to 27 h in 23 to 25 °C water (Rabalais et al. 1980). Dispersal occurs during the egg and early larval stages. Snapper larvae probably have a relatively short planktonic life (Randall and Brock 1960; Leis 1987). Larval snappers in coastal waters may prefer mid to deep water

during the day and move upwards at night to become more uniformly distributed (Powles 1977; Leis 1987).

Recruitment to snapper fisheries may depend on factors other than the abundance of larvae available to settle (Powles 1977). The availability of suitable habitat for juveniles and adults might limit recruitment independent of the numbers of larvae present. Survival of early benthic juveniles may also affect final recruitment to the fishery.

Juvenile red snapper have been captured over smooth sand or mud bottom which is regularly trawled for shrimp (Moseley 1966; Bradley and Bryan 1975; Grimes et al. 1977). Similarly, relatively flat, sand bottoms may provide essential habitat for the juvenile Hawaiian deepwater snappers *Pristipomoides filamentosus*, *Aphareus rutilans*, and *Aprion virescens* (Parrish 1989). More recent studies have shown that although juvenile red snapper are occasionally found on flat bottoms, most are associated with small structures, objects, or burrow openings (Workman and Foster 1994). Juvenile snapper recruitment to trawl-webbing reefs corresponded with bottom temperatures between 22 and 24 °C, and the smallest recruits were 12.7 mm FL (Workman et al. 1998a). The snapper in this study seemed to prefer the artificial reef habitat, but were deterred from the reef by agonistic behavior of one or two individuals. Other laboratory experiments have demonstrated that small juvenile red snapper prefer to live in more complex habitats, but avoid these structures because of aggressive behavior by larger juveniles and adults (Bailey 1995). Sub-adult red snapper also tended to be in close association with oil platform structure, whereas the adults did not appear to be obligate to structure (Render 1995).

Aggressive behavior of adult snapper may be an expression of dominance, or the larger snapper may actually be feeding on the smaller snapper. Bailey (1995)

noted that the larger snapper kept the young-of-the-year fish from artificial reefs with a minimal amount of chasing. Similarly, Mueller et al. (1994) found that large mutton snapper were more aggressive than smaller snapper and suggested that a few large mutton snapper may dominate the smaller snapper through social interactions. The presence of adult damselfish, *Pomacentrus amboinensis*, negatively affected the growth of juveniles, primarily the largest and behaviorally dominant individuals (Jones 1987). Although Bailey (1995) found no evidence of cannibalism in the adult red snapper he examined, it very likely does exist in nature. Cannibalism may be the driving force behind the evolution of ontogenetic changes in habitat use by some fish species, such as the threespine stickleback, *Gasterosteus aculeatus* (Foster et al. 1988). Cannibalism may be either heterocannibalism, where unrelated conspecifics are killed and consumed, or filial cannibalism, where kin are eaten (FitzGerald and Whoriskey 1992). Since red snapper eggs and larvae are pelagic, the offspring are typically swept away to other sites. Therefore, it is unlikely that adult and juvenile fish present on a site will be related (Sale 1978). Cannibalistic acts by adult snapper will be unlikely to reduce its genetic fitness because the predator and prey are probably unrelated (Hamilton 1964; Brown and Brown 1993).

Juveniles that are seen away from reefs and other bottom topographic features may be feeding. Food items of juvenile (and adult) snapper often include species associated with mud bottoms and not reef habitats (Davis 1975; Futch and Bruger 1976). Small (<40 mm) juvenile snapper feed primarily on zooplankton, including chaetognaths and larval crustaceans and fishes (Moseley 1966). Moseley noted that 40- to 90-mm snapper exhibit a slow shift in preference from zooplankton to macro-animals (cephalopods, crabs, juvenile shrimp and fishes). Bradley and Bryan (1975) reported that the transition period from zooplankton to juvenile crustaceans and other

fishes occurred in 101- to 150-mm snapper. Larger juveniles (and adults) appear to feed on whatever is available (Moseley 1966; Bradley and Bryan 1975).

Juveniles of most, or all, snapper species occur in shallower water than the adults (Rivas 1970). Although this is true for red snapper (Moseley 1966; Bradley and Bryan 1975), their distribution and abundance varies seasonally. Off Texas, juveniles were farthest offshore (38.4-64.0 m depths) in the winter and closest (20.1-27.4 m depths) in the summer (Bradley and Bryan 1975). As snapper grow and the weather becomes colder, they appear to move to deeper water, although after emigrating for the first winter, juveniles may return to shallower water during the spring and summer (Bradley and Bryan 1975; Gutherz and Pellegrin 1988). Although the red snapper is typically considered an offshore species, juveniles may occasionally enter high salinity estuaries. Ogren and Brusher (1977) reported the collection of 62 juvenile red snapper during the summer and fall of 1972-73 in the lower St. Andrew Bay system of Florida.

Monthly catches of red snapper in commercial trawls are highest from July through November and lowest from January to April (Gutherz and Pellegrin 1988; Goodyear and Phares 1990). Nichols (1989) reported that snapper appeared in about 50% of groundfish survey trawl samples. Densities of juvenile red snapper in the Gulf were highest off Texas, followed by Louisiana, in depths of 20.1 to 36.6 m (Gutherz and Pellegrin 1988). Catch rates of snapper were highest near 27 m, and catches were generally higher from 24 to 46 m (Nichols 1989). Both young-of-the-year and one-year-old red snapper are caught by trawls (Goodyear and Phares 1990).

Red snapper adults and larger juveniles may form schools near reef habitats (Davis 1975; Beaumariage and Bullock 1976), although they may range out over nearby soft-bottom habitat to feed (Moseley 1966; Futch and Bruger 1976). Sub-

adult (180 to 300 mm) snapper near an oil platform were observed in large schools of 30 to over 100 individuals whereas adults tended to be solitary or in small groups (Render 1995). These schools tend to disperse at dusk. Schools of a related species, *Lutjanus monostigma*, also tend to break up in the evening, apparently once a critical light level is reached (Potts 1970). Morrow (1948) noted that vision is the prime factor involved in the formation and maintenance of fish schools. Collette and Talbot (1972) reported that many species of snapper left the reef at dusk to feed, and although some fish were single, others apparently were still in schools.

Red snapper are facultative schoolers, fish that school temporarily because of environmental conditions or fright, or for activities such as feeding or reproduction (Breder 1967). Some of the reasons suggested for the formation of fish schools have included: protection from predators, improved feeding ability, energy conservation, and facilitation of reproduction.

Since red snapper are predators, the most likely reason adult snapper school is to improve feeding ability. Individuals in schools could benefit from the past experience and discoveries of other school members. When new Pacific sardines, *Sardinops caerulea*, were added to an existing school that had previously fed, the new school members acted entirely in unison with the school (O'Connell 1960). Schooling can be especially important when food is patchily distributed, such as when prey species school. Although individual jacks, *Caranx ignobilis*, were most successful at capturing isolated Hawaiian anchovy, *Stolephorus purpureus*, schooled jacks were more successful at capturing anchovy schools (Major 1978). Schooling acanthurids were found to have higher foraging rates than solitary individuals (Reinthal and Lewis 1986).

Another possibility is that the adult snapper school and make fertilization easier. Snappers typically spawn at dusk or at night (Grimes 1987), then schools break up and the snapper go away from the reefs to feed. The advantages of schooling for feeding could be less advantageous at night, or the prey species may be less susceptible to schooling behavior. However, it is unclear whether schooling to facilitates reproduction sufficiently to cause schooling to evolve (Wilson 1975).

A similar difference in schooling behavior between juvenile and adult red snapper was also reported in *Lutjanus monostigma* (Potts 1970). The juvenile snapper were frequently seen in small groups in shallow water, whereas the adults often formed schools of over a thousand individuals. As the fish increase in size, they typically change from facultative to obligate schooling (Potts1970). In contrast, although 80% percent of the known fish species school as juveniles, only 20% continue to school as adults (Burgess and Shaw 1979).

Schools of juvenile snapper were most frequently observed on larger reef structures. Juvenile snapper most likely school to reduce the chances of predation and possibly to facilitate feeding. Predators searching randomly are less likely to find prey that are spaced close together than prey that are spread out (Brock and Riffenburgh 1960; Major 1978). However, Hobson (1978) suggested that it was unrealistic to assume that predators or prey are distributed randomly and that certain large predatory reef fishes visit specific locations to feed.

Schooling may, however, improve the ability of prey species to detect predators. Schools of the spottail shiner, a facultative schooling species, had a shorter reaction distance than solitary shiners when faced with a predator (Seghers 1981). Once a school is detected, the presence of large numbers of fish may confuse the predators and make it more difficult for them to pick out individual prey

(Hobson 1978). Seghers (1974) suggested that schooling in guppies, *Poecilia reticulata*, may have developed in response to predation. However, Hobson (1978) noted that it is usually difficult to measure a selective advantage for aggregating by observing how often predators detect prey because predators and prey often remain within sight of one another for long periods without overtly interacting. Some species are simultaneously prey for larger fish and predators of smaller fish (Shaw 1978). This is likely the case for juvenile snapper, particularly the larger juveniles.

Aside from the schools of juveniles found near the low-relief reefs, juvenile snapper are typically found associated with small depressions and wormholes. These smaller habitat structures are probably able to shield only one or two snapper from predators. Similarly, Itzkowitz (1974) noted that in some reef species the juveniles tend to have smaller aggregations and hierarchies with aggressive behavior, whereas adults schooled and did not exhibit aggressive interactions. There are several possible functions for this territorial behavior. Dispersal may be increased if aggressive individuals force subordinates to seek shelter on other reef structures. This could reduce the chances of predation by distributing the snapper among the available protective habitats.

Another function of territorial behavior could be to spread the snapper out to take advantage of available resources. If resources are randomly distributed, this would enable the fish to take advantage of the resource availability. Patchy resources in an area could only be sufficient to support one or two snapper. Competition among juveniles could limit growth rates. For some species, competitive interactions that follow settlement determine growth rates of new juveniles and the delayed maturation increases juvenile mortality (Sale 1988). However, Doherty (1982) found no relation between density and mortality of damselfish, *Pomacentrus*

wardi and *P. flavicauda*, so competition within a year-class may not control the density of young fish in wild populations.

Bycatch Reduction of Young-of-the-Year Red Snapper

The territorial behavior of small juvenile red snapper may be a hindrance to reducing the numbers caught in shrimp trawls. It is possible that increasing the amount of trawl webbing in shrimp trawls, and the complexity of BRD's could potentially increase the retention of small red snapper. The snapper frequently tried to squeeze into enclosed areas, such as between a piece of rod and trawl webbing or places where trawl webbing overlapped. Devices that have nooks and crevices that entice juvenile snapper also have the potential for increasing retention of young snapper. Simpler devices may actually better improve the escapement of young-of-the-year red snapper.

Another possibility could be to place an object in the trawl that will move, since the moving decoys affected the snapper positioning, although this would primarily work during daylight hours unless it vibrates or elicits a pressure wave. Creating noise or vibration in a trawl could affect snapper escapement. However, when the captive snapper were subjected to noises or vibrations caused by tapping on the side of the tank, their startle response was to dive towards the sides of the tank, net, or corners of a bare tank. Startling the snapper may actually increase retention.

Since territorial behavior occurred under reduced water flow conditions, resulting in snapper getting behind the panels and staying, devices that do not reduce the water flow as much, such as the fisheye excluder, might be a better option for reducing young-of-the-year snapper.

If most snapper escape during haulback (Watson et al. 1993), devices that maintain the openings with fixed frames may be more effective (Rogers et al. 1997a).

Panels would most likely be ineffective unless they are positioned so that on haulback, fishes would be forced out an opening. However, this type of arrangement would very likely be accompanied by an increase in shrimp loss. If water velocities are slow in the codend of a trawl, and snapper go into the codend, they will be less likely to exit through escape openings unless during haulback the fish are forced forward.

Smaller snapper that are still able to swim during haulback could also potentially escape through the trawl meshes. During the preliminary experiments, five snapper passed through the trawl webbing surrounding the frame. Several of these individuals subsequently passed back through the webbing and re-entered the net. Increasing the mesh size could potentially improve reduction rates of the smallest snapper, however, this would undoubtedly be accompanied by increased shrimp losses, particularly of smaller shrimp. In addition, fish escaping through trawl meshes may be injured. Suuronen et al. (1996) reported that small Baltic herring, *Clupea harengus*, passing through codend meshes had a 7-day post-capture mortality of 72%. The mortality was most likely due to skin injuries and exhaustion.

The mortality rates of the snapper that escape these BRD's is currently unknown. If most snapper do escape during haulback, they are released higher up in the water column which may make them more susceptible to predation. Atlantic bottlenose dolphin, *Tursiops truncatus,* were regularly seen following trawls equipped with BRD's in a previous study in Louisiana (Rogers et al. 1994). Rulifson et al. (1992) reported that escapement through BRD's was influenced by predators. In their study, dolphin auditory noises caused Atlantic bumper, *Chloroscombrus chrysurus*, to tighten their school, maximizing their distance from escapement panel webbing. In addition, the duration of the tow and the length of time a snapper is

forced to swim within a trawl will affect their ability to evade predation. The more tired the fish is, the more likely it will be subject to increased mortality. Escaped fishes have typically been subjected to numerous capture stressors and could have been injured by contact with other fishes, debris, or the gear (Chopin and Arimoto 1995).

Of particular concern was the high mortality due to swim bladder expansion and other injuries of the young-of-the-year red snapper collected in this study. Mortality rates ranged from 50 to 90% for these snapper. These fish were brought slowly to the surface and were subjected to several decompression stops. Mortality occurred even when the snapper were brought to the surface at very slow rates (about an hour from 21 m to the surface). Rogers et al. (1986) reported that 55% of the red snapper trawled from 37 m depths had everted stomachs; when rapid retrieval systems were used, the value was 83%. This contrasts with the 9% eversions observed by Bradley and Bryan (1975) and 53% seen by Moseley (1966) in snapper trawled from similar depths.

Trawling depth appears to be a significant factor in mortality of red snapper. Snapper caught at depths less than 30 m in the study by Rogers et al. (1986) did not suffer significant trauma. However, the snapper for this study were collected from shallower depths. Other factors may be involved, such as the developmental stage of the snapper, water temperature differences between the bottom and the surface, or the effort exerted by the fish during capture. Smaller snapper could possibly be more susceptible to mortality from swim bladder expansion although none were observed to have everted stomachs in this study. A needle could be used to release air from many of the dying snapper, although this is not a preferred practice. Rogers et al. (1986) suggested that oral protrusions would likely result in high mortality rates

among subsequently released fish. Releasing snapper away from the bottom could potentially subject them to higher mortality even if they are not suffering from swim bladder expansion.

Snapper mortality during this study occurred up to three days after the fish were captured. Determining the latent mortality rates of fishes escaping BRD's would be difficult. Divers could collect the fishes that come out of the escape openings, since most escape is during haulback, they would have to follow the net up, collect the fishes, place them in cages, and observe the latent mortality. However, if escaped fishes are more susceptible to predation because of injury or fatigue, divers or Remotely Operated Vehicles (ROV's) would have to be used to observe the snapper after they escape from the trawls and count how many are eaten during a given period of time. Determining latent mortality rates could be extremely difficult since death could occur days from the time the fish is trawled and is affected by the degree of injury or stress incurred by the fish during the trawl and the necessary recovery period.

Since it is difficult to get young-of-the-year snapper to exit BRD's and mortality rates are unknown, BRD's may not be the solution to reduce bycatch mortality of very small snapper. Perhaps another tactic might prove better. The NMFS Harvesting Systems Branch in Pascagoula, Mississippi, has had success recruiting young-of-the-year red snapper to low-relief rubble, shell, and webbing reefs (Workman, et al., 1998 a,b). Workman et al. (1988a) found that snapper were most attracted to more complex webbing reefs, such as those with polyethylene strands tied at 15-cm intervals. Many of the snapper used in this study were collected from these reefs. Low-relief reefs would provide habitat structure for young snapper, but are less likely to be inhabited by larger fish that may prey on, or compete with, the

juvenile snapper. These reefs would also provide fish with refuge from shrimp trawls since shrimpers cannot operate on them. The juvenile snapper may not move around between reefs very often. Juvenile snapper were not found in the lanes between trawl-webbing reefs in one study (Workman et al. 1998a). Szedlemayer and Shipp (1994) found little movement in tagged juvenile snapper on artificial reefs off Alabama.

The use of low-relief reefs to provide habitat structure for juvenile red snapper off the Louisiana coast may be somewhat limited by the presence of the hypoxia zone in some places. The size of the area where dissolved oxygen levels are at or below 2 mg/L along the Louisiana coast may be as large as 9500 km^2 at its peak (Rabalais, et al. 1994, 1996). This area of hypoxia typically is present from May to mid-September, although in some years it may occur as early as February and as late as October (Rabalais, et al. 1994, 1996). However, the juvenile snapper in this study did recur on the reefs once the hypoxia zone had dissipated.

The webbing reefs were also quickly covered with a layer of fine silt. This suggests that rubble reefs may be more appropriate in areas with high accretion rates. Offshore waters near the location of the webbing reefs in this study had average accretion rates of 0.5 to 1 m for the period from 1930 to 1980 (List et al. 1994).

The placement of suitably designed low-relief reefs to provide sanctuary in key red snapper recruitment areas, coupled with the use of BRD designs that are effective for larger juveniles could benefit snapper populations.

Conclusions

These experiments indicate that agonistic behavior may reduce the ability of young-of-the-year red snapper to escape from BRD's that operate by creating areas

of reduced water flow near escape openings. Based on the results of these experiments, vertical and horizontal panels do not appear to be an effective mechanism to induce young-of-the-year red snapper to exit trawls. Although the panels created reduced-flow areas, these reduced flows appeared to trigger a territorial response in the young snapper. Frequently, one snapper would get behind a panel and prevent other snapper from entering the area. Therefore, access by the other snapper to the escape openings was limited.

The juvenile red snapper in the behavior experiments appeared to form dominance hierarchies in the absence of a reef habitat, and when they were excluded from the reef habitat by the resident territorial juvenile. The resident snapper in the reef tank were dominant both around and away from the reef and attacked nearly all the nonresidents (individuals not associated with the reef) in the tank at some point in the experiment. Agonistic activity among the nonresident snapper in the reef tank remained high when the experiment ended. The continual disruptions by the resident territorial snapper may have prevented stabilization of the dominance hierarchy among the nonresident individuals. In contrast, the number of overt agonistic acts declined over time when a constant number of snapper were maintained in the tank. These fish appeared to establish a dominance hierarchy quickly, requiring little subsequent agonistic activity to maintain the hierarchy. These laboratory results indicate that territoriality and dominance hierarchies may coexist in red snapper when reef habitats are easily defendable. Agonistic activity was higher under low-water-velocity conditions than under no flow because of the creation of a reduced-flow area.

The mortality rate of juvenile snapper escaping from BRD's is currently unknown. It is critical to determine this mortality rate to accurately determine how well BRD's are actually reducing bycatch. It is undoubtedly incorrect to assume that

100% percent of the snapper that are released from shrimp trawls survive, particularly fish that are trawled from deeper water. If trawl survival is indeed low, perhaps another technique, such as the use of low-relief rubble reefs may be more appropriate for enhancing recruitment rates of juvenile red snapper. Another possibility might be to identify juvenile snapper nursery areas and close these areas to shrimping. The use of habitat-enhancing reefs, in concert with other management techniques, may be necessary to reduce their susceptibility to trawls.

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VITA

Donna Reeve Rogers was born December 23, 1961, in Hunterdon County, New Jersey. Her interest in marine fisheries was cultivated at a very early age, and she spent much of her childhood in the outdoors hiking, fishing, and accompanying her father on hunting trips.

In 1983, she received a Bachelor of Arts degree in Biology from the University of South Florida, then spent several years working in marine fisheries at Mote Marine Laboratory in Sarasota, Florida. She left to attend graduate school at Louisiana State University and received a Master of Science degree in Fisheries in 1989, examining the effects of water control structures on marsh fishes. Before graduating, she accepted a position with the School of Forestry, Wildlife, and Fisheries at Louisiana State University and spent the next six years conducting fishery research. Initial research efforts focused on the effects of water-control structures on fishes in various coastal Louisiana marshes. She then developed an interest in shrimp trawl bycatch reduction and conducted a multi-year study to evaluate various bycatch reduction devices in inshore waters of Louisiana. This study led her to enroll in the doctoral program in Oceanography and Coastal Studies in 1994, where she has been studying the behavior of juvenile red snapper in relation to bycatch reduction.

DOCTORAL EXAMINATION AND DISSERTATION REPORT

Candidate: Donna Reeve Rogers

Major Field: Oceanography and Coastal Sciences

Title of Dissertation: Behavior of Red Snapper, Lutjanus campechanus, in Relation to Trawl Modifications to Reduce Shrimp Trawler Bycatch

Approved:

Major Professor and Chairman

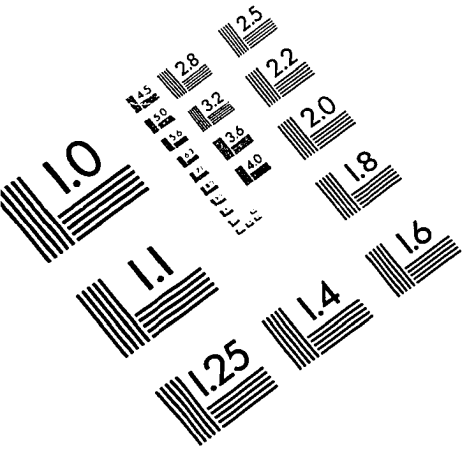
Dean of the Graduate School

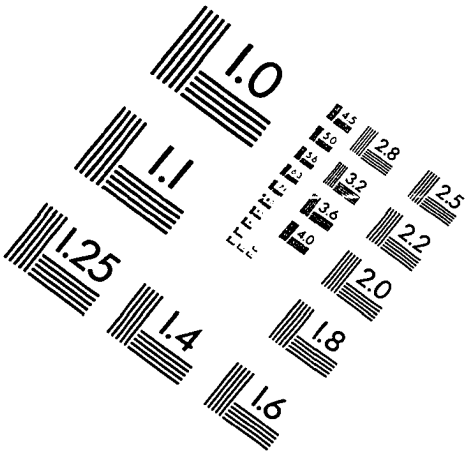
EXAMINING COMMITTEE:

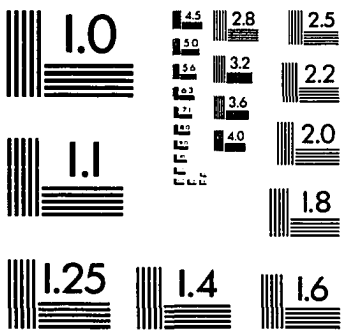
Date of Examination:

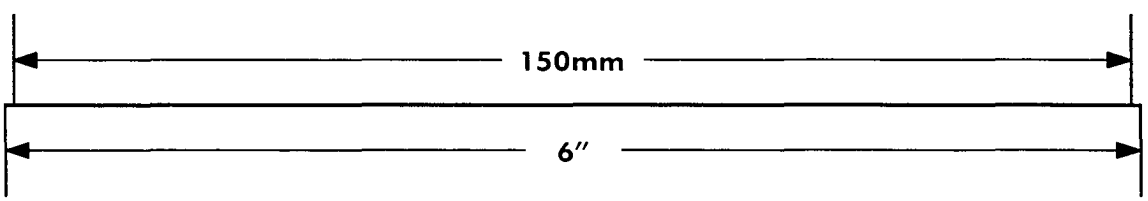
7/2/98

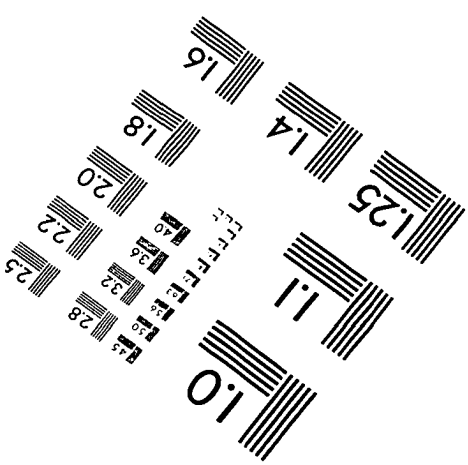
IMAGE EVALUATION
TEST TARGET (QA-3)











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